VARIATION AND ONTOGENY OF SOME OXFORD CLAY AMMONITES: *DISTICHOCERAS BICOSTATUM* (STAHL) AND *HORIOCERAS BAUGIERI* (D'ORBIGNY), FROM ENGLAND

by D. F. B. PALFRAMAN

ABSTRACT. Variational and ontogenetic studies of *Distichoceras bicostatum* (Stahl) and *Horioceras baugieri* (d'Orbigny) have shown identity in their early stages. Variation in protoconch size is consistent and small, as is the diameter of the nepionic construction. Divergence in shell form occurs only at the onset of maturity, which in *H. baugieri* begins at about 8–10 mm. and in *D. bicostatum* at about 30–35 mm. It is concluded that the two 'species' are a sexually dimorphic pair. The name *D. bicostatum* has priority.

NEITHER *Distichoceras bicostatum* (Stahl) nor *Horioceras baugieri* (d'Orbigny) appears to be plentiful in this country. Among the author's collection of several thousand ammonites from the Oxford Clay of Woodham, Bucks. (Arkell 1939 and Palframan 1966), only eight belonged to these species. From a locality not recorded in the literature as having typical Oxford Clay facies, but mentioned by Arkell (1945) as having crushed ammonites in a shale of Coronatum age, at Peckondale Hill, near Malton, Yorkshire (Grid. Ref. 745686), the author collected more than a thousand ammonites from the Athleta/Lamberti Zones of the Oxford Clay and found only three specimens of these species. The actual proportion of the ammonite fauna these two species occupy is generally not given, but from the numbers or frequency mentioned in the literature it would appear that they are at best rare and, more often, extremely rare.

Preservation. Almost all the specimens examined from the Oxford Clay of Eye, Woodham, Oxford, Dauntsey, and Tidmoor Point are preserved as internal pyrite moulds; in no specimen has the original shell been preserved. Some specimens from these localities and all those from Peckondale Hill are internal moulds of limonite. Because of the presumed physico-chemical factors which influenced preservation of many Oxford Clay ammonites, rarely are pyritic moulds to be found with a diameter greater than 2–3 cm. A notable exception to this is one superbly preserved phragmocone of *Distichoceras bicostatum* (Stahl), OUM J25688, from the Oxford Clay of Tidmoor Point, Dorset, which has a diameter of 5 cm. The body chamber, however, is almost entirely lacking (see Pl. 9, fig. 7*f*). Several small ammonites from the Oxford Clay, which are almost certainly the juvenile stages of *D. bicostatum*, have been found and it is these which furnish most of the information relating to the early ontogenetic stages mentioned here. The later ontogenetic stages, especially those of maturity, are largely based on specimens from the Hackness Rock of the Yorkshire Coast. Specimens from this bed are usually preserved to diameters of 4–7 cm. and are internal moulds composed of hard, slightly oolitic, limestone; in a very few cases tiny patches of shell material have been preserved, which appear to retain their original structure. The ammonites from the Hackness Rock often lacked body chambers and almost all had indifferently preserved inner whorls.

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Within the 70 ft. of Oxford Clay exposed at Woodham, Bucks., is a one-foot thick band of compact marly limestone, the 'Lamberti Limestone' of Arkell (1939—see this work for details of the exposure). The ammonites from this bed are generally poorly preserved internal moulds composed of the same material as the surrounding matrix and often crushed. The shell is commonly represented by a fine, powdery, black film covering the mould. Septa are, however, frequently preserved as relatively resistant calcite. The inner whorls of these ammonites are often broken, lacking or preserved as featureless recrystallized calcite, entirely unsuitable for ontogenetic studies. From the clays beneath the Lamberti Limestone are the familiar pyritic nuclei of about 2 cm. diameter.

Material. Altogether some 63 specimens belonging to these two species have been examined, 56 from England and 7, for comparative purposes, from Europe. They are recorded from the following localities:

Locality	*Specimen Number*	*Sex*	*Bed/Horizon*	*Collector*
1. Yorkshire				
a. Scarborough	BM 39525	♀	'Kellaway Rock', Callovian	W. Bean
	BM 50622	♀	Kellaways Rock, Callovian	J. Morris
	BM 89044	♀	Kellaways, Rock Callovian	J. S. Bowerbank
	BM C69282	♀	Scarborough Grey Limestone (Lamberti Zone)	L. F. Spath
	SM J5618–21	4 ♀ ♀	Kellaways Rock	J. Leckenby
	SM J47113	♀	Kellaways Rock	
b. Gristhorpe Bay	SM J5622	♀(?)	Kellaways Rock	J. Leckenby
	SM J5623	♀	Kellaways Rock	
c. Peckondale Hill	LU 263–4	2 ♀ ♀	Oxford Clay	D. F. B. Palframan
	LU 265	♂	Oxford Clay	D. F. B. Palframan
2. Eye, near Peterborough	BM C15708–BM C15712	2 ♂ ♂, 2jj 1 ♀(?)	Oxford Clay	E. T. Leeds
3. Woodham, Bucks.	OUM J14560	♂	Oxford Clay	R. A. Monkhouse
	OUM J20851–3	3 ♀ ♀	Oxford Clay, Lamberti Zone	W. J. Arkell
	OUM J20854	♀(?)	Oxford Clay, Lamberti Zone	W. J. Arkell
	OUM J25677–OUM J25684	4 ♂ ♂, 2jj	Oxford Clay	D. F. B. Palframan
	SM J34090–1	2 ♂ ♂(?)	Oxford Clay	N. F. Hughes
4. Oxford				
a. Summertown	OUM J20325	♀	Oxford Clay, Lamberti Zone	
	BM C10638	♂	Oxford Clay	
	BM C10644–6	3 ♂ ♂	Oxford Clay	
b. Cowley	OUM J23246–7	2 ♂ ♂	Oxford Clay	
5. Wiltshire				
a. Dauntsey	BM 27411	♀	Oxford Clay, Athleta Zone	W. Buy
	BM C72580–1	2 ♀ ♀(?)	Oxford Clay, Athleta Zone	W. Buy
b. nr. Chippenham	BM 37755	♂	Oxford Clay	W. Buy

Locality	Specimen Number	Sex	Bed/Horizon	Collector
6. Tidmoor Point, Dorset	OUM J25685–OUM J25688	1j, 1 ♂, 2 ♀ ♀	Oxford Clay, Lamberti Zone	M. R. House
	BM C28325–BM C28330	2jj, 2 ♂ ♂, 2 ♀ ♀(?)	Oxford Clay	R. H. Cunnington
	BM C28351	♀(?)	Oxford Clay	R. H. Cunnington
7. Ecrouvres, nr. Toul, France	SM F16204	j	'Oxford Clay'	J. D. Hudson
8. Trockau, Bavaria, Germany	BM C40979–80	2 ♀ ♀	Divesian (*lamberti* beds)	E. Model
	BM C40982	♂	Divesian, (*lamberti* beds)	E. Model
9. Beuren, Württemberg, Germany	BM C73642–4	3 ♂ ♂	Brown Jura ζ	

Abbreviations. The following prefixes denote the institutes from which the specimens were borrowed: OUM—Oxford University Museum; BM—British Museum (Natural History); SM—Sedgwick Museum, Cambridge; LU—Department of Geology, University of Leicester. The '*Bed/Horizon*' listed above has been transcribed from the labels accompanying the specimens. The stratigraphy of the species concerned will be considered in a later chapter. In the column '*Sex*', above, 'j' denotes juvenile specimens, sex indeterminate. Due to very poor preservation there is some doubt about the identification of specimen SM J5622 (Gristhorpe Bay).

VARIATION AND ONTOGENY OF *DISTICHOCERAS BICOSTATUM* (STAHL)

It is considered in this paper that *Distichoceras bicostatum* (Stahl) is the female of a dimorphic pair and is therefore referred to as *D. bicostatum* ♀.

Family OPPELIIDAE Bonarelli 1894
Subfamily DISTICHOCERATINAE Hyatt 1900
[= BONARELLIDAE Spath 1925]
Genus DISTICHOCERAS Munier-Chalmas 1892

Type species. Ammonites bipartitus Zieten.

Synonym. Bonarellia Cossman 1898, p. 77.

Type species. Ammonites bicostata Stahl

Distichoceras bicostatum (Stahl) ♀

Plate 9, figs. 8*a–c*, 7*a–i*, 8; Plate 11, figs. 3*a–d*, 4*a–c*, 5*a–b*, 7*a–b*, 8*a–b*; Plate 12, figs. 3, 5, 6*a–b*, 7*a–b*, 8*a–c*, 9*a–b*; Plate 13, figs. 1*a–e*, 2, 3: text-figs. 1–5, 7–9.

1824 *Ammonites bicostata* Stahl, p. 49, fig. 9*a–c*.
1830 *Ammonites bipartitus*; Zieten, p. 18, pl. 13, fig. 6.
1830 *Ammonites calcar*; Zieten, p. 18, pl. 13, fig. 7.
1842–51 *Ammonites bipartitus* (pars); d'Orbigny, p. 443, pl. 158, figs. 1, 2, 4.
1852 *Ammonites bipartitus*; Quenstedt, p. 367, pl. 28, fig. 9.
1858 *Ammonites bipartitus*; Quenstedt, p. 530, pl. 70, fig. 11.
1886–7 *Ammonites bipartitus* (pars); Quenstedt, p. 732, pl. 85, figs. 1–5, 7–8, 23, 25–27.
1899 *Bonarellia bicostata*; Crick, p. 554, figs. 1–2.
1902 *Bonarellia bicostata*: Crick, p. 47.

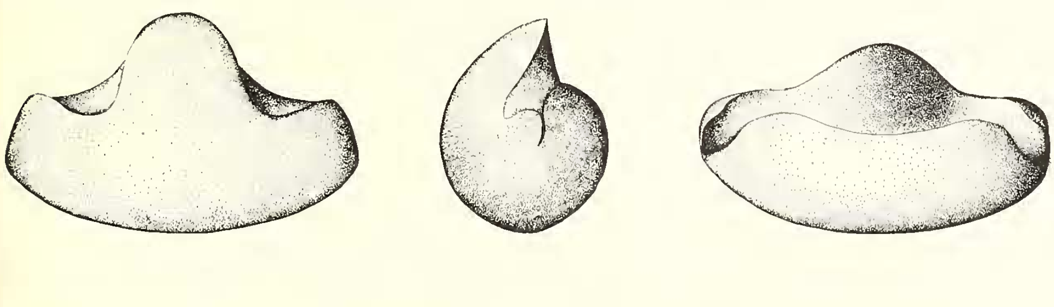
1914 *Oppelia* (*Distichoceras*) *bipartita* (pars); Douvillé, p. 17, pl. 5, figs. 19, 19*a*, 20, 20*a*, text-fig. 11.
1927–33 *Bonarellia bicostata*; Spath (part ii, 1928), p. 95, pl. 15, figs. 4*a–c*.
1927–33 *Bonarellia* sp. ind. Spath (part ii, 1928), p. 95, pl. 14, figs. 2*a–c*.
1938 *Distichoceras nodulosum* Maire, p. 45, pl. 2, figs. 2, 2*a*.
1938 *Distichoceras subornatum* Maire, p. 46, pl. 3, figs. 19, 19*a*.
1939 *Distichoceras bicostatum*; Arkell, p. 167, pl. 8, figs. 19*a*, 19*b*.
1951 *Bonarellia bicostata*; Jeannet, p. 36, pl. 8, figs. 1–5, text-figs. 81, 82.
1957 *Distichoceras bipartitum*; Arkell, Kummel, and Wright, p. L279, fig. 327, 1*a–b*.
1963 *Distichoceras bicostatum*; Callomon, p. 42, fig. 9 M.
1963 *Distichoceras bipartitum*; Schindewolf, p. 380, fig. 228.

General remarks and diagnosis. Because of the preservation of Upper Callovian ammonites in this country, just mentioned, the problem of studying the variation and ontogeny of ammonites with a diameter greater than 2–3 cm. is twofold. Firstly, to acquire material which has well-preserved juvenile and adult stages (in this paper the two growth stages are examined from specimens of different beds and/or different localities) and secondly to be sure that the juvenile and adult ammonites are conspecific. It is therefore necessary that the larger diameters of juvenile ammonites (pyritic, Oxford Clay type preservation) are greater than the smallest preserved diameters of adults (the more or less complete ammonites of the Hackness Rock and Lamberti Limestone type preservation).

Distichoceras bicostatum (Stahl) ♀ is a fairly typical oppelid, being compressed and involuted. Whorl height (HH) is generally half the diameter (D), whorl width (W) between one-third and one-quarter the diameter. The umbilicus is small, except in the final stages of maturity when the umbilical seam begins to uncoil. The innermost whorls are smooth; later phragmocone whorls have small ventro-lateral spines with looped ribs. The body chamber is weakly ribbed and without spines and about five-eighths of a whorl in length and terminated by a simple peristome.

PROTOCONCH

Only one protoconch (OUM J25681) was available for measurement, D 0·27 mm., W 0·44 mm. However, a poorly preserved specimen BM C15712 (labelled '*Distichoceras* juv.'), is almost certainly *D. bicostatum* ♀ and furnished a beautifully preserved



A B C

TEXT-FIG. 1. Protoconch of *Distichoceras bicostatum* (Stahl). Diagram based on juvenile male (?) from the Lamberti Zone, Tidmoor Point, Dorset, England: OUM J25687. A, ventral view; B, side view; C, apertural view. All figs. ×100.

protoconch with the following dimensions, D 0·24 mm., W 0·40 mm. (see Table 1). The protoconchs, both internal pyrite moulds, are perfectly smooth (see text-fig. 1) and clearly show the nature of the proseptum and prosuture (Schindewolf 1954). They are extremely elongate and barrel-shaped with a W/D ratio of about 1·65. Since the early works of Branco (1879–80, 1880–1), little has appeared on the nature and measurements of protoconchs and details of the young stages of oppelid ammonites are generally lacking. However, for *Creniceras renggeri* (Oppel) ♂ and ♀, the W/D ratio is about 1·45 (Palframan 1966).

PHRAGMOCONE

Early whorls and general growth pattern. The first whorl of growth from the proseptum is smooth and depressed; it is terminated by the nepionic constriction which occurs at a diameter of 0·49 mm. (see Table 1). The nepionic constriction is clearly defined; it is strongest ventrally and ventro-laterally, weakening on the flanks and almost completely fading at the umbilical seam (see text-fig. 2). There is no evidence of the nepionic constriction, on internal moulds, in the dorsal region. The juvenile whorls immediately succeeding the nepionic constriction are perfectly smooth.

As growth progresses from the protoconch, the whorls of the juvenile stages become less depressed (cf. text-figs. 1 and 2B), the W/D ratio decreasing markedly (see text-fig. 7A). At a diameter of about 2 mm. the whorl section is subquadrate becoming higher as growth progresses. Whorl heightening is accompanied by a flattening of the flanks which converge towards the venter, itself altering from rounded to tabulate at a diameter

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EXPLANATION OF PLATE 9

Distichoceras bicostatum (Stahl)

Fig. 1. Juvenile female from the Lamberti Zone, Tidmoor Point, Dorset, England: BM C28325. *a*, side view of the innermost whorls; *b*, apertural view of innermost whorls; *c*, side view of inner whorls; *d*, apertural view of inner whorls.

Fig. 2. Juvenile male from the Athleta/Lamberti Zone, Woodham, Bucks., England: OUM J14560. *a*, side view, the last quarter whorl is body chamber, note the sinuous elevation (see also text-fig. 6B); *b*, ventral view, note the relatively large spines and adoral weakening of the ventral ridge.

Fig. 3. Male from the Athleta/Lamberti Zone, Woodham, Bucks., England: OUM J25677. Phragmocone with approximated sutures. *a*, side view; *b*, ventral view, note absence of ventral ridge.

Fig. 4. Juvenile male, from the Athleta/Lamberti Zone, Woodham, Bucks., England: OUM J25679. Side view of immature phragmocone.

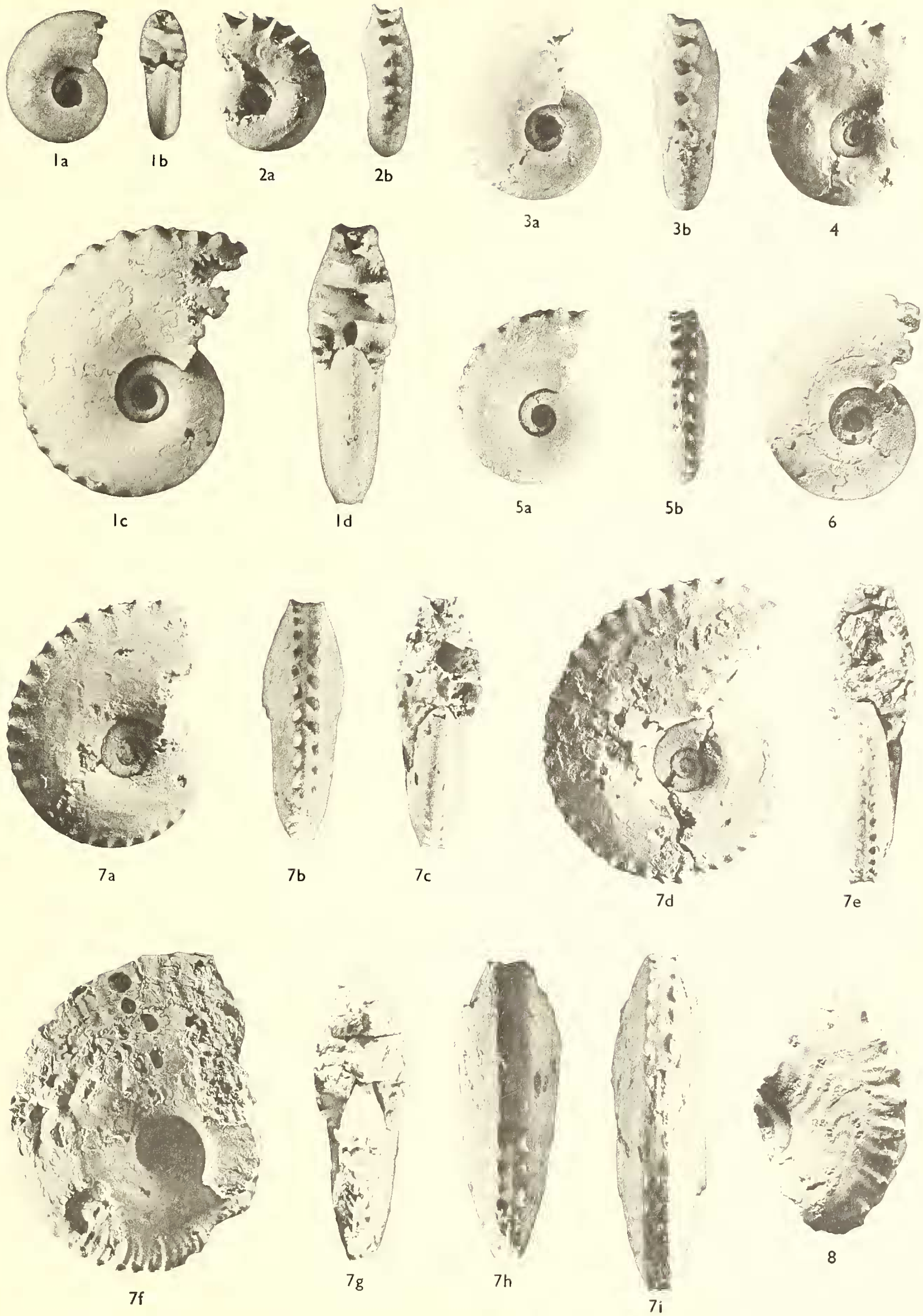
Fig. 5. Juvenile male(?) from the Lamberti Zone, Tidmoor Point, Dorset, England: OUM J25687. Immature phragmocone. *a*, side view; *b*, ventral view, note the feeble ventral ridge.

Fig. 6. Juvenile male(?) from the Athleta/Lamberti Zone, Woodham, Bucks., England: SM J34091. Immature phragmocone.

Fig. 7. Female from the Lamberti Zone, Tidmoor Point, Dorset, England: OUM J25688. *a–e*, preparations of the inner whorls; *f–i*, the phragmocone of the adult. *a*, side view; *b*, ventral view, note the continuity of the ventral ridge; *c*, apertural view; *d*, side view, note the development of looped ribs; *e*, apertural view; *f*, side view, note sutural approximation, degeneration of looped ribs and slight uncoiling at the umbilical seam of the body chamber (quarter of a whorl partially preserved); *g*, apertural view; *h*, ventral view, note degeneration of the ventral ridge and ventro-lateral spines; *i*, ventral view. *d–e* ×2, *f–i* ×1.

Fig. 8. Juvenile female(?) from the Lamberti Limestone, Woodham, Bucks., England: OUM J20854. Immature phragmocone showing the beginning of looped ribs and ribbing on the lower flank.

All figures ×3 unless otherwise stated. Specimens have been whitened with ammonium chloride. Photographs by the author, all un-retouched.

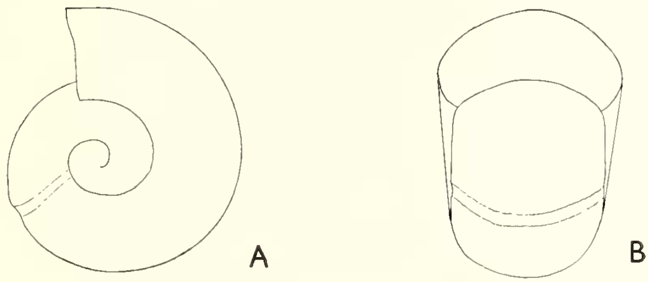


PALFRAMAN, *Distichoceras* from the Oxford Clay

of 5–7 mm. The change in whorl shape from this diameter can be seen in preparations of specimens OUM J25688 (Pl. 9, figs. 7*c*, *e*, and *g*) and BM C28325 (Pl. 9, figs. 1*b* and *d*). From a diameter of 6–10 mm., the umbilical wall steepens appreciably, almost at right angles to the median plane, accompanied by a well-marked umbilical shoulder (see text-figs. 7A and D) which remains pronounced on to the body chamber.

From a diameter of about 1 mm. to just beyond the adoral end of the phragmocone, the W/D, U/D, and HH/D ratios reflect almost isometric growth (see text-figs. 3, 4, and 5).

Remarks. The first whorl of growth, the nepionic whorl of Westermann (1958), is always smooth among ammonites so far investigated. After the nepionic constriction the juvenile whorls of *Creniceras renggeri* (Oppel) ♂ and ♀ have been shown to be



TEXT-FIG. 2. The innermost whorls of *Distichoceras bicostatum* (Stahl). Drawn from a female(?) from the Athleta/Lamberti Zone, Woodham, Bucks., England: OUM J25681. The position of the nepionic constriction can be seen. Both figs. $\times 50$.

smooth (Palframan 1966). However, Makowski (1962) has shown that the ornament characterizing the adult shell of *Kosmoceras* and *Garantiana* appears immediately after the nepionic constriction.

Ornament. At a diameter of 5–7 mm. the venter becomes tabulate (text-fig. 7A), this feature heralding the beginning of true ornamentation. At this diameter three morphological features may develop, either altogether, in pairs, or singly. The usual sequence following ventral tabulation appears to be:

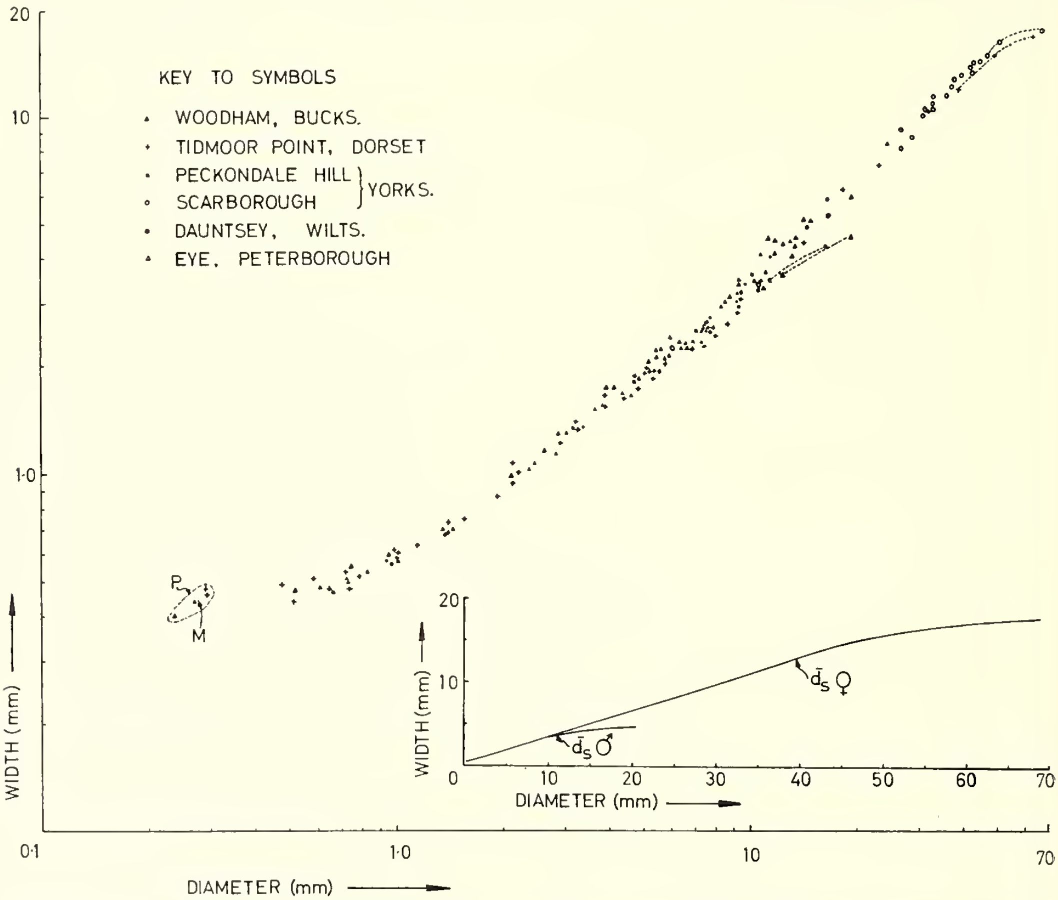
(*a*) The development of ventro-lateral spines. These are small and alternate either side of the venter, they generally number about 35–40 (each side of the venter) in the early stages (Pl. 9, figs. 7*b*–*e*) and have a well-defined beginning (Pl. 9, fig. 7*c* and Pl. 11, fig. 4*c*).

(*b*) The development of a ventral ridge, or carina. This usually begins at the same diameter as the ventro-lateral spines, but may begin at a slightly later growth stage (Pl. 9, figs. 7*b*, *c* and Pl. 11, figs. 4*b*, *c*, and 5*b*). (*b*) is never developed before (*a*).

(*c*) The development of lateral ornament. This is confined to the mid-flanks and generally develops at larger diameters than are recorded for the beginning of ventro-lateral spines or ventral ridges and may take the form of a fillet or groove.

At diameters larger than 7 mm. other ornamental features may develop: these will be mentioned later.

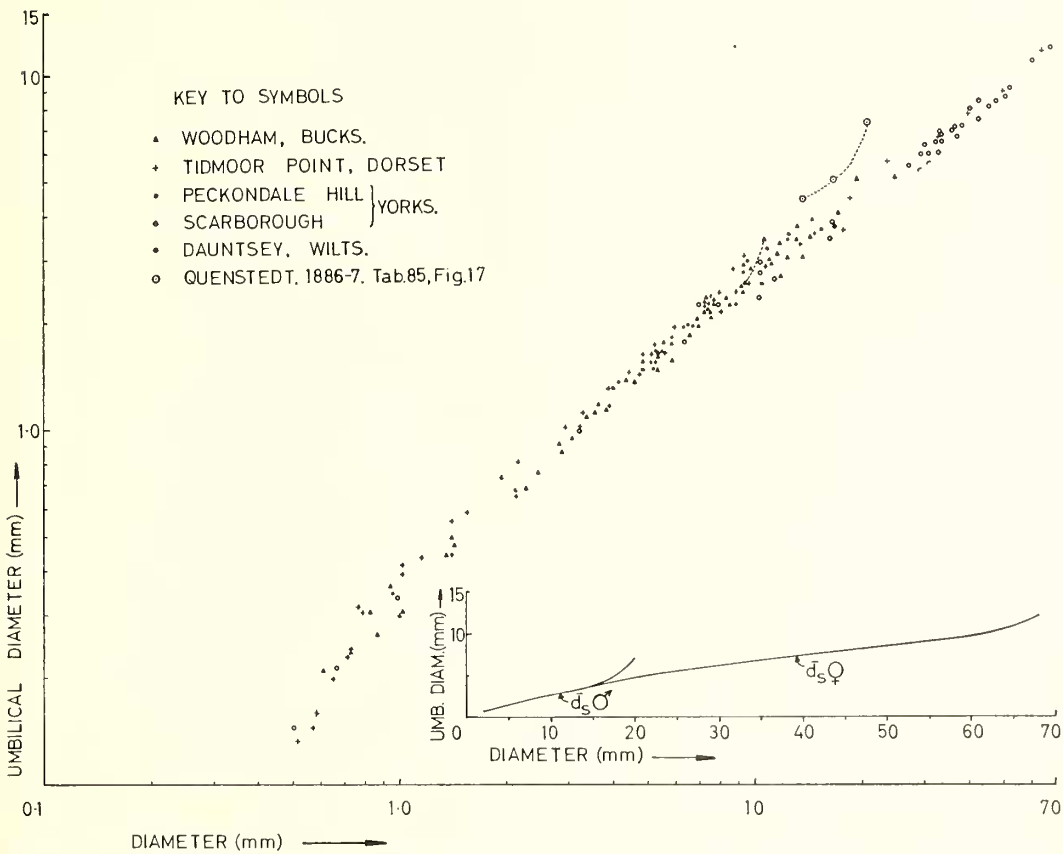
Ventro-lateral spines. The growth and size of ventro-lateral spines appear to be directly proportional to the diameter of the shell: they number about 40 per whorl on the mature phragmocone as in specimen OUM J25688 (Pl. 9, fig. 7*f*). The number of spines per whorl in the late stages of development ranges from 30, SM J5618 (not figured), to 50, SM



TEXT-FIG. 3. Graph showing the relationship between Diameter and Width of *Distichoceras bicostatum* (Stahl) ♂ and ♀. Dashed lines connect recordings made on the same specimen. The area P (dot-dash line) encloses measurements made on the protoconchs, M is the mean of these measurements. Inset, the same graph plotted on a linear scale, showing the plot of the approximate best-fit line. The arrowed points $\bar{d}_s$ ♂ and $\bar{d}_s$ ♀ represent the position of the mean diameter at which septation ceases in mature specimens of male and female respectively.

J5621 (Pl. 11, figs. 7*a*, *b*), among the specimens examined. Beyond a diameter of 12–20 mm., the ventro-lateral spines are related to ribs which develop on the ventral half of the flank.

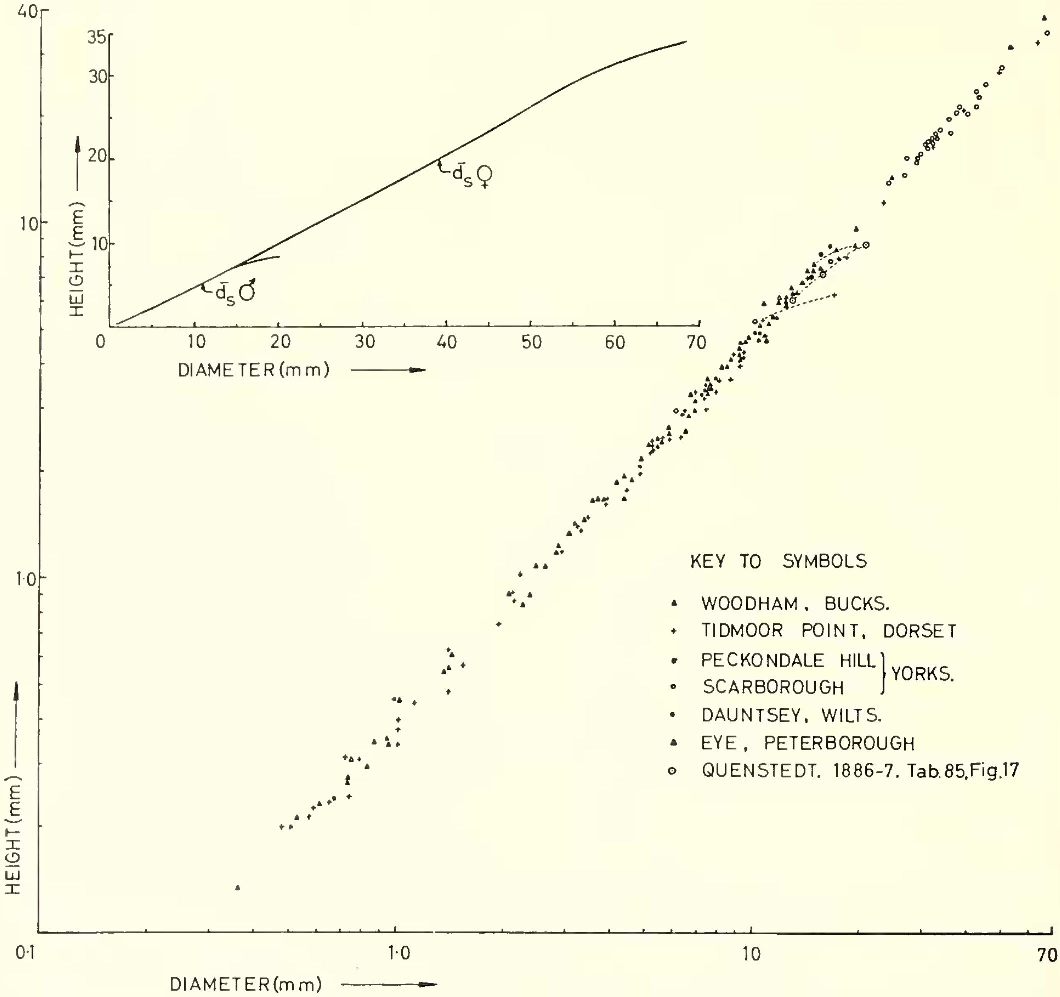
Ventral ridge. The ventral ridge, or keel, undergoes little modification during the growth of the phragmocone. It is concomitant with the ventro-lateral spines and easily visible at either the same diameter of spine development or at a slightly larger diameter. The ontogeny of the ventral ridge is summarized in Plate 9 (figs. 7*b*, *c*, *e*, *g–i*), beginning feebly in the juvenile stages, becoming stronger adorally, and finally weakening towards the end of the phragmocone with the degeneration of the ventro-lateral spines. From the earliest stage the ridge may be straight (Pl. 9, fig. 7*b*) or wrinkled (Pl. 11, fig. 4*b*). In the late ontogenetic stages of the phragmocone, among the majority of the specimens



TEXT-FIG. 4. Graph showing the relationship between Diameter and Umbilical Diameter of *Disticho-ceras bicostatum* (Stahl) ♂ and ♀. Dashed lines connect recordings made on the same specimen. Inset, the same graph plotted on a linear scale, showing the plot of the approximate best-fit line. The arrowed points $\bar{d}_s$ ♂ and $\bar{d}_s$ ♀ represent the position of the mean diameter at which septation ceased in mature specimens of male and female respectively.

examined, the ventral ridge is nearly always wrinkled to a greater or lesser degree (Pl. 11, fig. 7*b*; Pl. 11, figs. 6*a*, 7*b*, 8*a*, and 9*b*) but may exceptionally be straight (Pl. 11, fig. 8*b*).

Lateral ornament. The lateral ornament, which frequently interrupts the ribbing, may take the form of either a fillet or groove or a combination of the two. In all stages of development the lateral ornament is usually only seen under conditions of low-angled lighting and is weakest in the earliest growth stages. A very feeble fillet can be seen on the juvenile preparation of specimen OUM J25688 (Pl. 9, fig. 7*d*) and a shallow groove on specimen OUM J20854 (Pl. 9, fig. 8). During adolescent growth the fillet may develop quite strongly (Pl. 12, fig. 6*b* and Pl. 13, fig. 2), but generally fades on the final quarter whorl of the phragmocone. The same is true of lateral grooves (Pl. 12, fig. 3). In specimen BM 89044, the lateral groove is very pronounced and bordered by levee-like fillets (Pl. 12, fig. 8*b*). A slight thickening of the ribs in mid-flank gives a third variation of lateral ornament, as shown by specimen SM J47113, that of a bullate spiral (Pl. 11, fig. 7*a*).

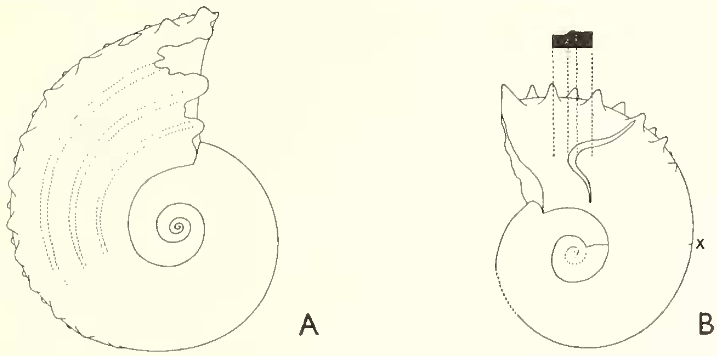


TEXT-FIG. 5. Graph showing the relationship between Diameter and Height of *Distichoceras bicostatum* (Stahl) ♂ and ♀. Dashed lines connect recordings made on the same specimen. Inset, the same graph plotted on a linear scale, showing the plot of the approximate best-fit line. The arrowed points $\bar{d}_s$ ♂ and $\bar{d}_s$ ♀ represent the position of the mean diameter at which septation ceased in mature specimens of male and female respectively.

Two rather delicate forms of ornament seen only on one juvenile specimen, OUM J25684, are spiral striae and small crescentic pits. The spiral striae are strongest near the umbilical shoulder becoming progressively weaker ventrally and fading altogether in the ventro-lateral region. On the mid-flank of the same specimen is a spiral series of small, shallow, convex, crescentic pits (Pl. 11, figs. 3*c*, *d*).

Remarks. The spiral striae and crescentic pits, just mentioned, may be impressions of shell ornament or, possibly, impressions of muscle attachments.

Ribbing. The earliest development of ribbing is at a diameter of about 12–13 mm. (OUM J20854, see Pl. 9, fig. 8). Each ventro-lateral spine is associated with a looped rib with no independent ribs between (Pl. 9, fig. 7*d*). The looped ribs are rursiradial (Pl. 9, figs. 7*f* and 8; Pl. 11, fig. 7*a*; and Pl. 12, figs. 3, 5, 6*b*, 7*a*, 8*b*, and 9*a*), though in the early stages of specimen OUM J25688 (Pl. 9, fig. 7*d*) only feebly so. In a few cases infrequent, single (non-looped) ribs are connected with individual ventro-lateral spines (Pl. 12, fig. 6*b*) and in one case there are independent ribs not connected with ventro-lateral spines (Pl. 12, fig. 7*a*). These cases are almost certainly 'normal exceptions' within the species under consideration. In the later stages of phragmocone growth the ribs of

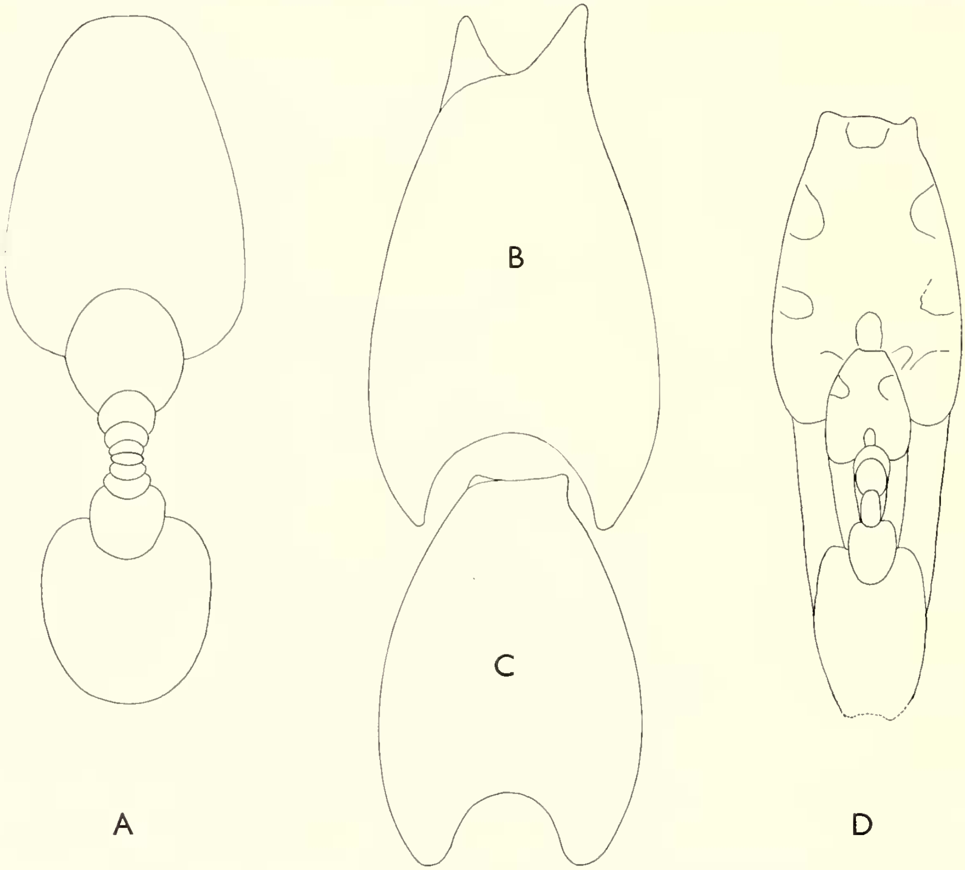


TEXT-FIG. 6. Ornamentation in *Distichoceras bicostatum* (Stahl). A, juvenile male(?) from the Lamberti Zone, Tidmoor Point, Dorset, England, showing three narrow fillets with wide grooves between: OUM J25687. B, juvenile male from the Athleta/Lamberti Zone, Woodham, Bucks., England: OUM J14560. The point *x* marks the position of the last suture. The sinuous elevation may represent a muscle-scar (see also Pl. 9, fig. 2*a*). Both figs. $\times 5$.

the ventral flank and the ventro-lateral spines become somewhat degenerate. The spines become indistinct and the ribs at this stage do not appear to be looped or intimately associated with the spines (Pl. 9, figs. 7*f* and *h*).

Ribbing on the ventral flank is never very strong and is best seen under low-angled lighting. Rib strength may be weak (SM J5621, Pl. 11, fig. 8*a*) to relatively strong (BM C69282, Pl. 13, fig. 2). In the early growth stages ribbing is almost entirely confined to the ventral portion of the flanks: in one observed case, OUM J20854, ribbing is also present on the lower, or dorsal, portion of the flank at a diameter of about 13 mm. (Pl. 9, fig. 8). From the material studied this certainly appears to be atypical, most specimens do not develop this inner ribbing until a much later stage in their ontogeny. Generally, in mature individuals, this feature develops on the final quarter whorl of the phragmocone (Pl. 11, fig. 8*a*).

On the dorsal portion of the flank the ribbing is quite strongly prorsiradial, but towards a mid-flank position becomes rectiradial or even rursiradial (Pl. 9, fig. 8 and Pl. 11, fig. 8*a*). These lower ribs are usually separated from the upper by some form of spiral ornament situated on the mid-flank. They are related to the upper ribs in their early development, in that each lower rib is opposite an upper looped rib. Towards the adoral end of the mature phragmocone, where the ventro-lateral spines become degenerate and in consequence the upper ribs are not looped, the lower and upper ribs are paired. This is more easily observed when the spiral ornament, which separates the upper and lower ribs, fades towards the end of the phragmocone and the ribs are



TEXT-FIG. 7. Cross-sections through *Distichoceras bicostatum* (Stahl). A, juvenile from the Athleta(?) Zone, Eye, near Peterborough, England: BM C15712. Specimen entirely septate; note the tabulation of the venter on the final preserved whorl. B, male from the Athleta/Lamberti Zone, Woodham, Bucks., England: OUM J25680. Drawn at D = 12·4 mm. (maximum septate diameter of adult). C, juvenile female(?) from the Athleta/Lamberti Zone, Woodham, Bucks., England: OUM J25681. Drawn at D = 11·1 mm. D, juvenile female from the Hackness Rock, Scarborough, Yorks., England: BM 89044. Section through immature phragmocone. Figs. A, B, and C, ×10, fig. D, ×3.

continuous across the whole flank (Pl. 12, fig. 3). The rib-type of the phragmocone immediately before the body chamber in mature specimens is convex to biconcave or sinuous (Arkell 1957*a*, p. L89).

Sutures

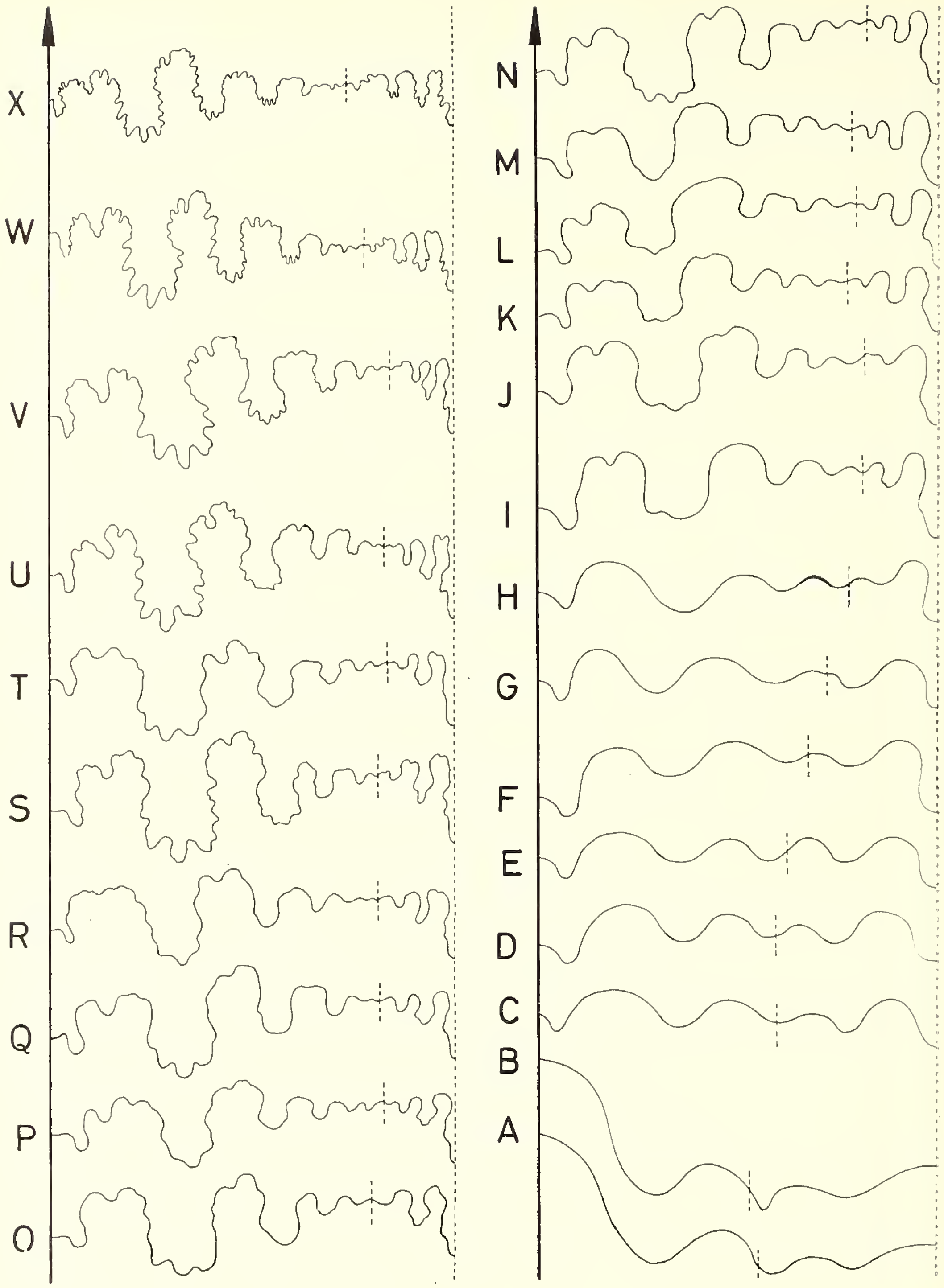
Sutural ontogeny. The sutural ontogeny of *D. bicostatum* ♀ is best illustrated diagrammatically (text-fig. 8). The succession of sutures (A–X) comprising the sutural ontogeny of text-fig. 8, is determined solely by increasing order of the diameter at which the sutures were drawn (from several different specimens). Because of individual variation and growth-rates, adjacent sutures (in text-fig. 8) drawn at similar diameters but from different specimens may not in fact reflect a true sutural ontogeny and would better conform by being reversed (as S and T in text-fig. 8). It should also be noted that text-fig. 8 is a composite sutural ontogeny of both supposed males and females of *D. bicostatum*, the presumed sex of each specimen from which a suture was drawn being denoted in the text-fig. caption. The addition of new sutural elements occurs at the umbilical seam, 'U-type ontogeny' of Schindewolf (1954).

Remarks. As the works of Schindewolf (1954, 1960, 1962, and 1963) have shown, there is a basic pattern according to which the sutural ontogeny of Jurassic ammonites can seemingly be predicted. This is, briefly, the formation of a septum closing the protoconch (proseptum) which at its margin gives rise to the prosuture with a predominantly large ventral saddle. This first-formed suture is very different from all succeeding sutures which are simply elaborations on the second-formed suture (primary suture). The primary suture is composed of more or less equally sized elements, the lobes being: external (or ventral), lateral, U_2, U_1, and dorsal. This is the quinquelobate basic suture of Schindewolf (1954). *D. bicostatum* ♀ conforms to this pattern as shown by Schindewolf (1963, p. 407, fig. 228) and herein text-fig. 8.

Sutural variation. In order to assess qualitatively the sutural variation at a prescribed diameter, the most ornate and variable elements of the suture (ventral and lateral lobe and first and second lateral saddles) from three randomly chosen specimens were drawn at a diameter of about 38 mm. Sutural differences either side of the venter in any single specimen are extremely small and such differences are, in part, influenced by the position of the ventro-lateral spines or interference by earlier formed septa (see text-fig. 9). Differences between the sutures of the three specimens are more marked and are probably influenced by the absolute diameter at which they were drawn (in text-fig. 9, A is drawn at a smaller diameter, 38 mm., than C, 38·5 mm.).

Remarks. Another factor which may influence the variation seen is that of absolute size of the phragmocone of the adult specimen. Ventral tubercles on the phragmocone of *Creniceras renggeri* (Oppel) ♂ and ♀ do not develop until the last quarter whorl of the phragmocone in mature specimens irrespective of the size of the phragmocone (Palframan 1966). As Makowski (1962) has pointed out, the diameter at which certain features develop is dependent on the stage of growth of an individual and not its size. This may also be true of sutures which have a level of complexity, or development, for a prescribed diameter which is influenced by the ultimate size of the phragmocone of the mature specimen. In other words, a small mature specimen of an ammonite species may have slightly more advanced sutures at any prescribed diameter than a larger specimen of the same species at the same diameter. Even so the final sutures of the smaller specimen will almost certainly be less complex than the final sutures of the larger specimen. A third factor influencing sutural differences may well be one of evolution as the material examined here almost certainly extends over two ammonite zones (Athleta and Lamberti). Finally, the variation may be in part geographic.

The sutures of specimen OUM J25684 from Woodham, Bucks., here considered as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being a juvenile form of *D. bicostatum* ♀, are irregularly spaced (see Pl. 11, figs. 3*c* and *d*). This spacing may be due to any one, or a combination, of several factors which may affect the growth-rate: (*a*) relative abundance/scarcity of food, (*b*) variable salinity or temperature of the sea-water, (*c*) disease, (*d*) periods of reproductive activity. The number of sutures on the final preserved whorl of the specimen in question is eight compared with twelve for other specimens of a similar size: BM C28325 (Pl. 9, fig. 1*c*) and OUM J25681 (Pl. 11, fig. 4*a*). Two pairs of adjacent sutures on specimen OUM J25684 are closely spaced, at diameters of about 7 mm. and 10 mm. respectively. The range of sutural approximation observed for ten specimens of *Horioceras baugieri* (d'Orbigny) (which in this paper is considered as being *D. bicostatum* ♂) is 8·7 mm. to 16·7 mm. It may be that the specimen in question (OUM J25684) has changed sex during life as do some living molluscs. The latter explanation is considered unlikely, though as this feature has not been seen in other specimens studied here, the explanation of the phenomenon is itself, no doubt, unusual.

The mature phragmocone. Sutural approximation and degeneration is regarded as a feature of maturity throughout this paper, along with other points generally considered as denoting maturity and listed by Callomon (1957). These are: uncoiling of the body chamber at the umbilical seam, modification of ornament, and the development of apertural modification such as lappets, rostra, and constrictions. The mean diameter at which septation ceases in mature specimens was found to be 39·5 mm. with a range of 31·5 to 49·7 mm. A phragmocone of *D. bicostatum* ♀ figured by R. Douvillé (1914, Pl. 5, figs. 20 and 20*a*) at 'grandeur naturelle', has a diameter of about 70 mm. The author has seen a plaster cast of this specimen in L'Ecole des Mines, Paris and verifies the size.

From the composite phragmocone ontogeny constructed it is estimated that from the prosuture to the beginning of the body chamber in *D. bicostatum* ♀ there are 7–7½ complete whorls. On no phragmocone did the author see original shell material.

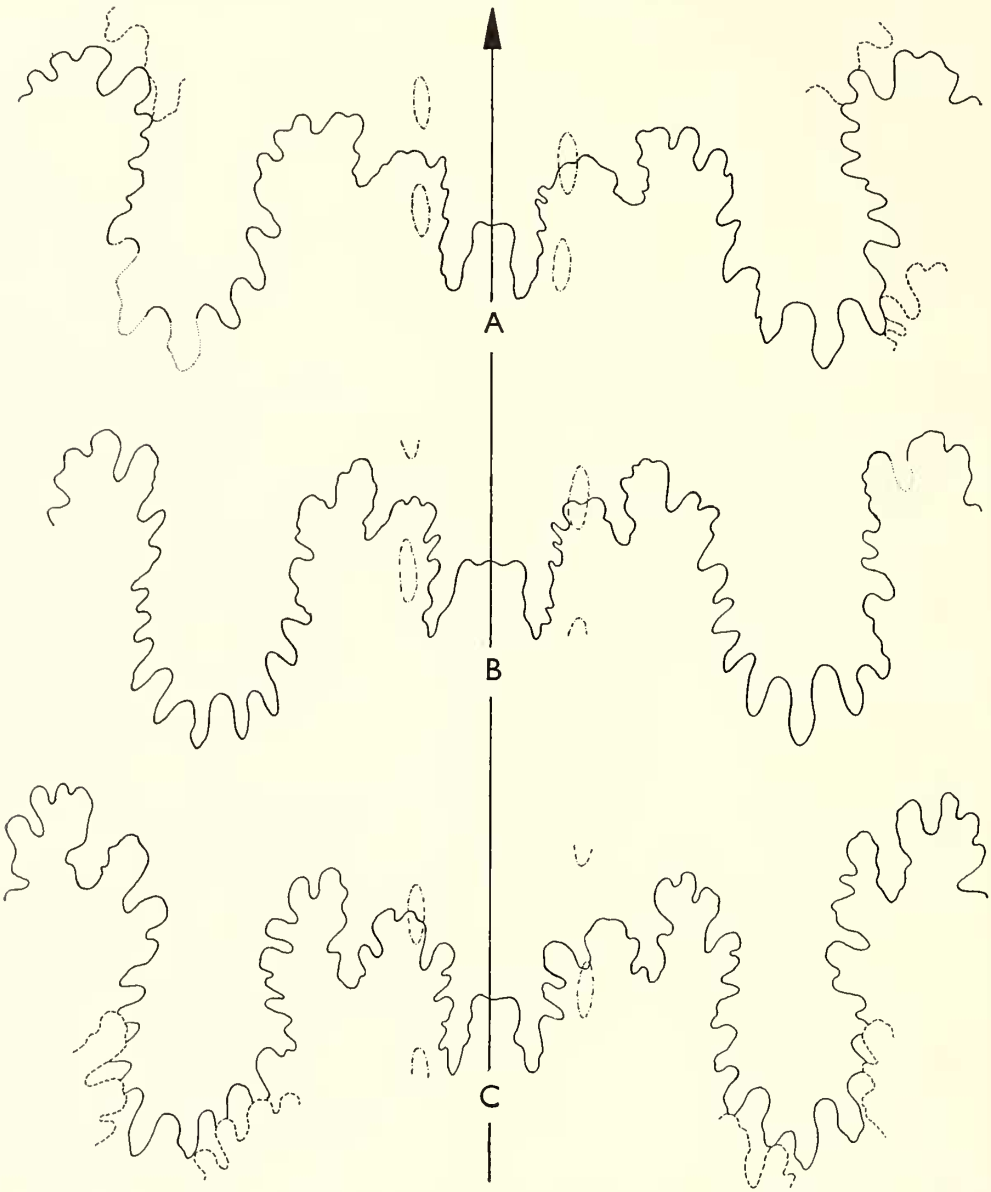
BODY CHAMBER

The following description of the body chamber rests almost entirely on two specimens, one from the Hackness Rock of Scarborough, Yorks. (BM 50622), the other from the Lamberti Limestone of Woodham, Bucks. (OUM J20851); the former being complete, the latter with a damaged aperture.

TEXT-FIG. 8. Sutural ontogeny of *Distichoceras bicostatum* (Stahl). A, prosuture, BM C15712, female(?), D = 0·24 mm. ×136; B, prosuture, OUM J25687, male(?), D = 0·29 mm. ×120; C, primary suture, OUM J25681, female(?), D = 0·29 mm. ×120; D, primary suture, OUM J25687, male(?), D = 0·31 mm. ×115; E, female(?), OUM J25681, D = 0·61 mm. ×100; F, female(?), OUM J25681, D = 0·77 mm. ×91; G, male(?), OUM J25687, D = 1·01 mm. ×71; H, female, OUM J25688, D = 2·21 mm. ×38; I, female(?), OUM J25681, D = 2·92 mm. ×34; J, female(?), OUM J25681, D = 4·17 mm. ×23; K, male, OUM J25677, D = 4·75 mm. ×18; L, juvenile, OUM J25686, D = 5·04 mm. ×17; M, male(?), OUM J25679, D = 5·4 mm. ×17; N, juvenile, OUM J25682, D = 5·8 mm. ×16; O, female(?), OUM J25681, D = 6·3 mm. ×14; P, juvenile, OUM J25683, D = 6·8 mm. ×13; Q, female, OUM J25688, D = 7·3 mm. ×12; R, male, OUM J25677, D = 8·2 mm. ×10; S, female(?), OUM J25681, D = 10·1 mm. ×8·3; T, male, OUM J25680, D = 11·0 mm. ×8·1; U, female(?), OUM J25685, D = 15·5 mm. ×5·7; V, female, OUM J25688, D = 16·0 mm. ×5·6; W, female, OUM J25688, D = 26·5 mm. ×2·9; X, female, OUM J25688, D = 45 mm. ×1·6. For localities and horizons see chart in text. The order of succession (A–X) is determined solely by the increasing diameter at which each suture was drawn.

General growth

The umbilical wall retains its steepness and the umbilical seam begins to uncoil but not markedly (Pl. 9, fig. 7*f* and Pl. 13, figs. 1*a* and 2): this is best shown graphically (text-



TEXT-FIG. 9. Sutural variation in *Distichoceras bicostatum* (Stahl). Females: A, OUM J25688 at D = 38 mm. from the Lamberti Zone, Tidmoor Point, Dorset, England; B, BM 39525 at D = 38·2 mm. from the Hackness Rock, Scarborough, Yorkshire, England; C, BM 50622 at D = 38·5 mm. from the Hackness Rock, Scarborough, Yorkshire, England. The positions of spines (dot-dash lines) and adjacent sutures (dashed lines) are clearly marked. All figs. ×5.

fig. 4). The W/D and HH/D ratios show negative allometry in the final growth stages of the body chamber (text-figs. 3 and 5). With only one complete specimen as evidence, the body chamber extends for a little more than half a whorl, bringing the total number of whorls from the proseptum to an estimated $7\frac{1}{2}$–$8\frac{1}{2}$.

Ornament

Ribbing. Many of the morphological features of the phragmocone are lacking or degenerate on the body chamber. The venter, though remaining tabulate, loses the ventro-lateral spines and ventral ridge, the transformation occurring either immediately before the end of the phragmocone (see Pl. 9, fig. 7*h*) or on the earliest part of the body chamber (see Pl. 13, figs. 1*b–c* and 3). As a result of the degeneration of the ventro-lateral spines, the ribs are no longer looped and, due to the absence of the lateral ornament, continue uninterrupted to the umbilical shoulder where they fade. The ribs of the body chamber are of the same form as those of the phragmocone, essentially sinuous (see Pl. 12, fig. 3 and Pl. 13, fig. 1*a*). Ribbing on the early part of the body chamber is fairly dense, becoming more distant and finally dense again near the peristome (see Pl. 13, figs. 1*a* and 3). The ribbing of specimen OUM J20851 is strong on the ventro-lateral area, weakening on the flanks, and not extending as far as the umbilical shoulder. Parallel to the ribs and best seen on the ventro-lateral area are fine growth lines (see Pl. 13, fig. 1*a*).

In the final growth stages ribbing becomes denser; the peristome assumes the outline of the rib-form but with slightly greater ventral prorsiradiation, forming a small rostrum to an otherwise simple peristome (BM 50622 see Pl. 13, figs. 1*a*, *d*). On the same specimen the ribbing crosses the venter of the body chamber, but is weaker ventrally than ventro-laterally (see Pl. 13, fig. 1*b*).

Lateral ornament. The spiral or lateral ornament, which generally fades towards the end of the phragmocone, is retained almost to the end of the body chamber in the form of a rather indistinct fillet in specimen BM 50622 (see Pl. 13, fig. 1*a*), but in this case does not interrupt the lateral ribbing.

Remarks. No consistent (thus discounting the lateral fillet/groove) morphological feature was seen which could be interpreted as a muscle scar, nor is there a feature which the author considered to be an annulus (Crick 1898). The latter feature may, however, have been masked by the vagaries of preservation. The annulus has been noted in other oppelid ammonites (Crick 1898 and Palframan 1966), but in these cases the mode of preservation was different, usually as internal pyritic moulds.

All the material examined has been in the form of internal moulds; in the case of specimen BM 50622, patches of shell material remain. These are probably inner shell layers and show feather structure (see Pl. 13, fig. 1*e*), a feature which has been recorded on other oppelid ammonites (Arkell 1957*a* and Hölder 1955). These patches of shell, even in the ventro-lateral and ventral regions, show precisely the same ornament as is shown by the internal mould and include such features as the weak lateral fillet and fading ventral ridge.

As far as the author is able to determine there do not appear to be any significant differences, in the early stages of ontogeny, between specimens of *D. bicostatum* ♀ from the localities previously listed, nor between preparations of the juvenile stages of undoubted specimens of this species and a collection of nuclei which is identical with the early stages of both *D. bicostatum* (= *D. bicostatum* ♀) and *Horioceras baugieri* (d'Orbigny) (= *D. bicostatum* ♂) as is shown in Table 1. The later growth stages described here depend almost entirely on specimens from the Hackness Rock of the Yorkshire coast, but a large specimen from Tidmoor Point, Dorset, and three large specimens from Woodham, Bucks., agree very closely in all respects with those from Yorkshire.

VARIATION AND ONTOGENY OF *HORIOCERAS BAUGIERI* (D'ORBIGNY)

(It is considered in this article that *Horioceras baugieri* (d'Orbigny) is the male of a dimorphic pair and is here referred to as *Distichoceras bicostatum* (Stahl) ♂.)

Family OPPELIIDAE Bonarelli 1894
Subfamily DISTICHOCERATINAE Hyatt 1900
[= BONARELLIDAE Spath 1925]
Genus HORIOCERAS Munier-Chalmas 1892,

Type species. Ammonites baugieri d'Orbigny 1842–9.

Distichoceras bicostatum (Stahl) ♂

Plate 9, figs. 2*a–b*, 3*a–b*, 4, 5(?)*a–b*, 6(?); Plate 10, figs. 1*a–d*, 2*a–c*, 3*a–c*, 4*a–c*; Plate 11, figs, 1, 2, 6; Plate 12, figs. 1, 2, 4; text-figs. 1(?), 3–5, 6, 7(?), 8, 10, 11.

1842–51 *Ammonites baugieri*; d'Orbigny, p. 445, pl. 158, figs. 5–7.
1852 *Ammonites bidentatus*; Quenstedt, p. 367, pl. 28, fig. 8.
1858 *Ammonites bidentatus*; Quenstedt, p. 531, pl. 70, fig. 10.
1886–7 *Ammonites bidentatus*; Quenstedt, p. 736, pl. 85, figs. 16–22, 24.
1898 *Distichoceras baugieri*; Crick, p. 100, pl. 20, fig. 8.
1914 *Oppelia* (*Horioceras*) *baugieri* (pars); Douvillé, R., p. 16, fig. 10, pl. 5, figs. 17, 21, 21*b*, 22, 22*a*.

EXPLANATION OF PLATE 10

Distichoceras bicostatum (Stahl)

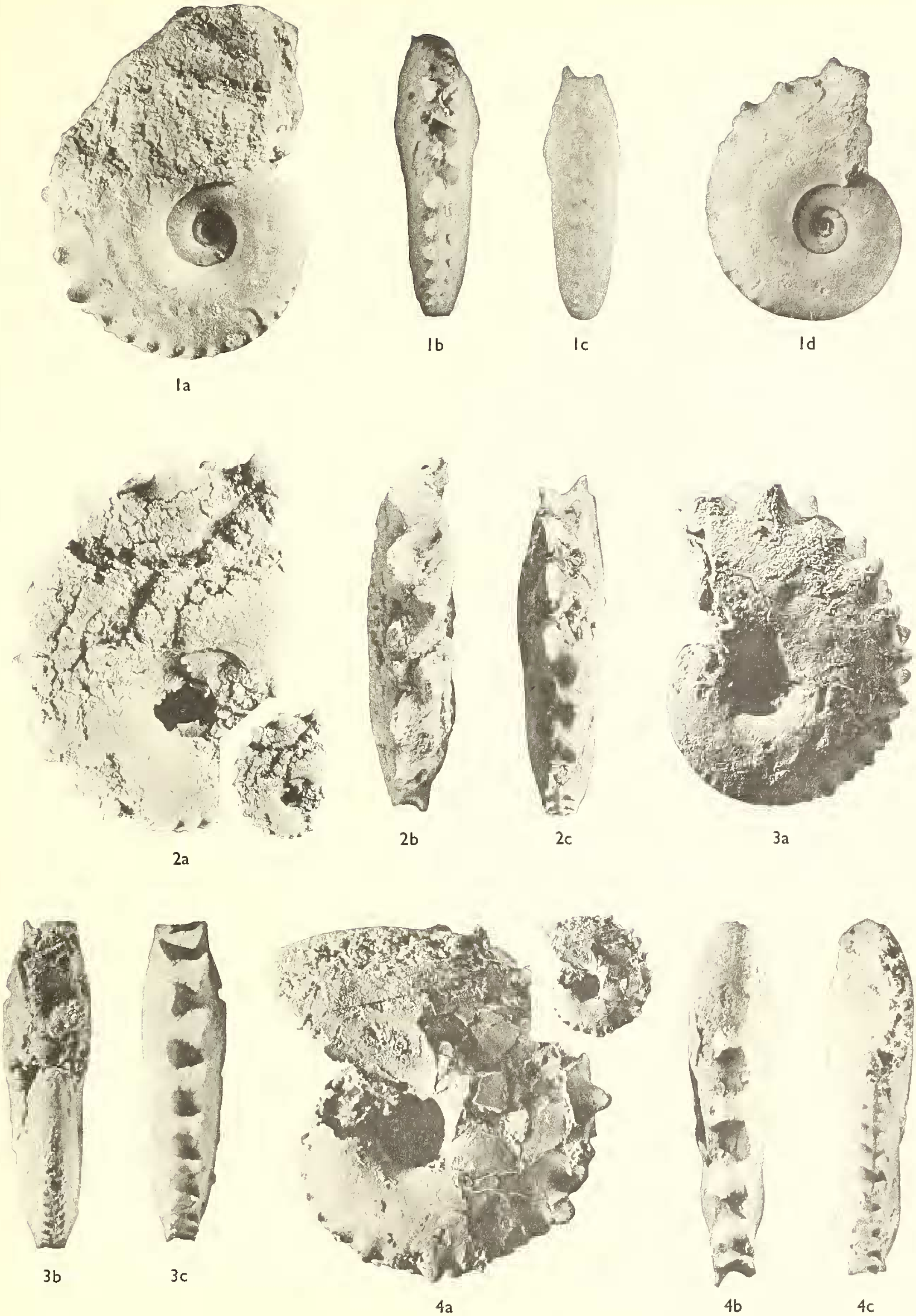
Fig. 1. Male from the Oxford Clay of Eye, near Peterborough, England: BM C15710. Mature phragmocone with a quarter of a whorl of body chamber. *a*, side view, note lateral groove; *b*, ventral view, note degeneration of the ventral ridge and relative increase in spine size adorally; *c*, ventral view; *d*, preparation of the phragmocone (cf. Plate 9, figs. 1*c* and 7*a*).

Fig. 2. Male from the Athleta/Lamberti Zone of Woodham, Bucks., England: OUM J25680. Mature specimen showing one-third of a whorl of body chamber. *a*, side view, note approximation of sutures and uncoiling of the body chamber at the umbilical seam; *b*, ventral view of body chamber, note the complete loss of the ventral ridge and the enormity of the ventro-lateral spines; *c*, ventral view, the most adapical part shows the presence of the ventral ridge. Inset ×1.

Fig. 3. Male from the Athleta/Lamberti Zone, Peckondale Hill, near Malton, Yorkshire, England: LU 265. Mature specimen with a third of a whorl of body chamber. *a*, side view, note sutural approximation and small crescentic pits on the flank; *b*, apertural view; *c*, ventral view.

Fig. 4. Male from the Athleta/Lamberti Zone of Woodham, Bucks., England: SM J34090. Almost complete adult specimen with a little more than half a whorl of body chamber. *a*, side view, note the complete fading of the spines on the body chamber, the presence of spiral ornament, and the uncoiling of the body chamber at the umbilical seam; *b*, ventral view, note the absence of the ventral ridge; *c*, apertural view, note the presence of the ventral ridge. Inset ×1.

All figures ×3 unless otherwise stated. Specimens have been whitened with ammonium chloride. Photographs by the author, all un-retouched.



PALFRAMAN, *Distichoceras* from the Oxford Clay

1927–33 *Horioceras baugieri*; Spath (part vi, 1933), p. 668, pl. 125, figs. 13, 14.
1957 *Horioceras baugieri*; Arkell, Kummel and Wright, p. L279, figs. 327, 3*a*.
1963 *Horioceras baugieri*; Callomon, p. 42, fig. 9*m*.
1963 *Horioceras baugieri*; Schindewolf, p. 406, figs. 229, 230.

General remarks and diagnosis. Mature specimens of *D. bicostatum* ♂ do not appear to grow beyond a maximum diameter of 2–3 cm., in consequence they are often preserved almost entire as internal pyritic moulds in the Oxford Clay at many localities. Because of its relatively small size it does not appear to be preserved in either the Lamberti Limestone of Woodham, Bucks., or the Hackness Rock of Yorkshire. In both these strata the inner whorls of most ammonites seem to be either poorly preserved, recrystallized and structureless, or entirely lacking beneath a diameter of 2–3 cm., which means that the chances of preservation of *D. bicostatum* ♂ are extremely slender.

The basic shape of *D. bicostatum* ♂ is rather eclipsed by the enormous ventro-lateral spines which develop on the last whorl of mature specimens. It is, however, moderately involute with a whorl width $\frac{1}{3}$–$\frac{1}{4}$ the diameter and a whorl height about half the diameter. The umbilicus is small but widens appreciably, due to uncoiling at the umbilical seam, on the body chamber of adult specimens. The innermost whorls are smooth; the last whorl of the phragmocone develops ventro-lateral spines and a ventral ridge. The latter fades at the end of the phragmocone as the spines become relatively larger. The body chamber is initially spinose but towards the end is smooth and terminated by a lappeted peristome.

PROTOCONCH

Only one protoconch from *D. bicostatum* ♂ has been obtained; its dimensions are very similar to those of *D. bicostatum* ♀. Altogether five protoconchs from the species under consideration have been obtained (from males and females): the size range is as follows: D, 0·24 to 0·30 mm., W, 0·40 to 0·48 mm. (see Table 1). Text-fig. 1 is drawn from *D. bicostatum* ♂(?), OUM J25687, showing the nature of the prosuture and general shape.

Remarks. The range in protoconch size though small is greater than that recorded for another oppelid ammonite species, *Creniceras renggeri* (Oppel) (Palframan 1966). However, the species examined here has been collected from a much wider stratigraphical and geographical range than the localized *C. renggeri* (op. cit.), and this almost certainly influences the observed variation.

PHRAGMOCONE

Early whorls and general growth pattern

From the proseptum the first whorl of growth is smooth and depressed and terminated by the nepionic constriction. In specimen BM C28329 the nepionic constriction does not occur until a little after one whorl of growth, at a diameter of 0·57 mm. The diameter at which the nepionic constriction occurs ranges, in *D. bicostatum* ♂, from 0·48 to 0·57 mm. The nepionic constriction is strongest ventrally and ventro-laterally, weakening on the flanks and fading completely near the umbilical seam (cf. text-fig. 2). No morphological feature is present in the early whorls until a diameter of between 5–7 mm. The extremely wide and depressed whorl outline of the protoconch (cf. text-fig. 1) alters markedly within the space of one whorl of growth (cf. text-fig. 2) and rapidly becomes subquadrate at a diameter of about 2 mm. Beyond this size the flanks flatten and begin to converge towards the venter. Ventral tabulation occurs at a diameter of about 5–7 mm., almost immediately before the first true ornament, and continues to the end of the phragmocone (see text-fig. 7A–B). From a diameter of about 1 mm. to near the adoral end of the phragmocone the W/D, U/D, and HH/D ratios remain almost constant, reflecting more or less isometric growth. Throughout there is no marked umbilical shoulder and the umbilical wall is consequently rounded.

Remarks. Two measurements of the diameter of the nepionic constriction, one from *D. bicostatum* ♀ and another from a juvenile specimen, are recorded and both fall within the range of the same measurement of *D. bicostatum* ♂ (see Table 1).

Ornament

At a diameter of 5–7 mm. the whorls, which up to this stage are smooth, develop ornament of the following nature: ventro-lateral spines, a ventral ridge, and lateral ornament. The ventro-lateral spines and ventral ridge usually begin together, as shown by specimen BM C28329 (see Table 1), or the ventral ridge may develop at a slightly later growth stage than the spines. The lateral ornament usually begins at about the same diameter as the ventro-lateral spines and may precede them (Pl. 9, fig. 6), begin at the same diameter (Pl. 9, fig. 3*a*), or succeed the ventro-lateral spines (Pl. 11, fig. 2).

Ventro-lateral spines. The ventro-lateral spines of *D. bicostatum* ♂ are identical in

EXPLANATION OF PLATE 11

Distichoceras bicostatum (Stahl)

Fig. 1. Juvenile(?) male, from the Oxford Clay of Summertown, Oxford, England: BM C10638. The specimen may be adult, but the final sutures do not appear to be approximated. The body chamber (final half whorl) is, however, beginning to uncoil at the umbilical seam. Side view showing about five complete whorls; the protoconch is absent.

Fig. 2. Male from the Lamberti Zone, Tidmoor Point, Dorset, England: BM C28327. Mature specimen with one-eighth of a whorl of body chamber. Side view, note sutural approximation.

Fig. 3. Juvenile female(?) from the Athleta/Lamberti Zone, Woodham, Bucks., England: OUM J25684. Immature phragmocone. *a*, ventral view (venter poorly preserved); *b*, apertural view; *c*, side view, note the irregular spacing of the sutures; *d*, as *c*, enlarged (×5) to show the spiral striae and sculpturing of the flanks.

Fig. 4. Juvenile female(?) from the Athleta/Lamberti Zone of Woodham, Bucks., England: OUM J25681. Immature phragmocone. *a*, side view; *b*, ventral view, note the continuous ventral ridge; *c*, apertural view.

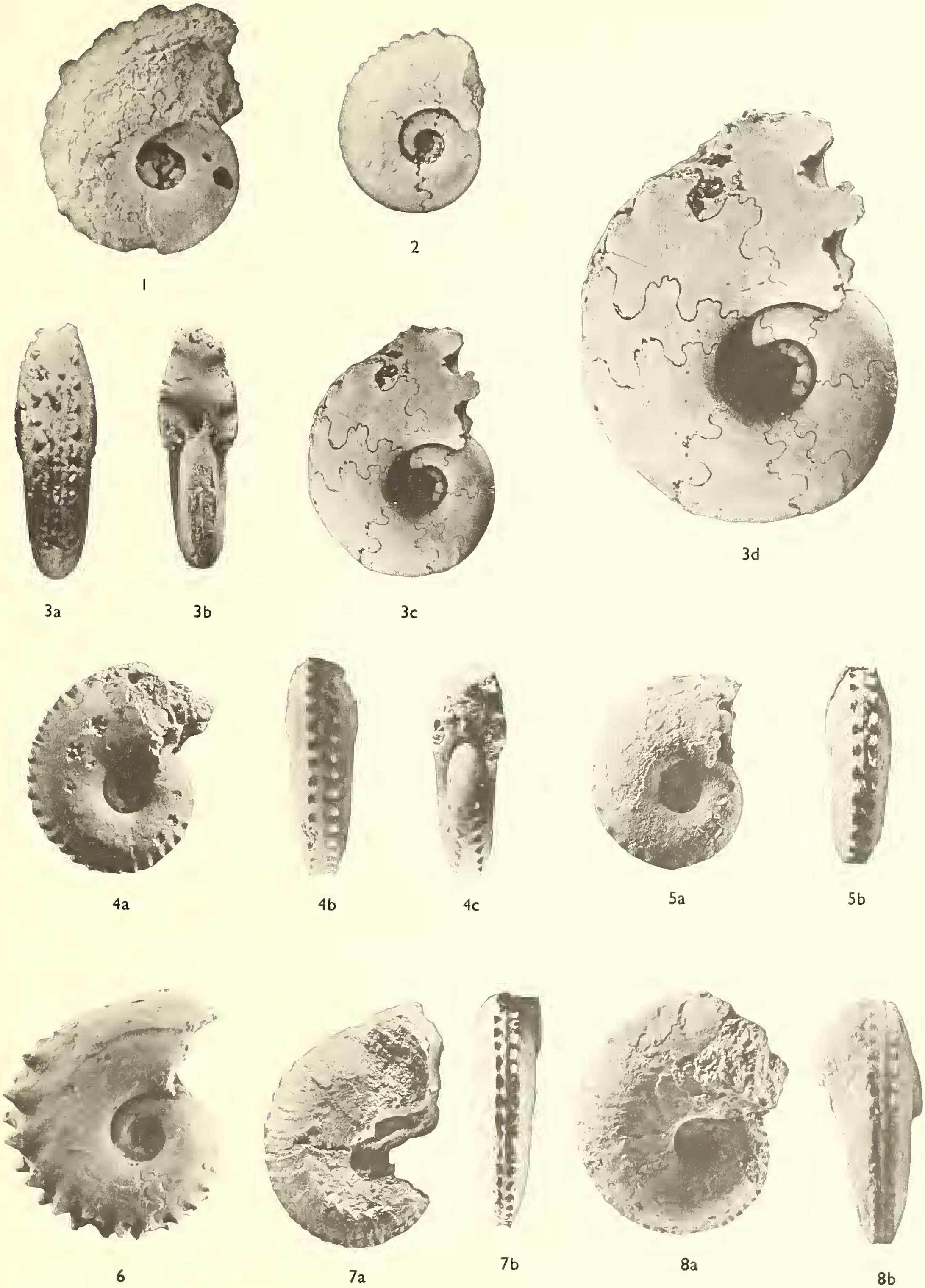
Fig. 5. Juvenile female(?) from the Athleta/Lamberti Zone of Peckondale Hill, near Malton, Yorkshire, England: LU264. Immature phragmocone. *a*, side view; *b*, ventral view, note the continuous ventral ridge.

Fig. 6. Male from the Oxford Clay, near Chippenham, Wiltshire, England: BM 37755. Side view, the final five-eighths of a whorl is body chamber.

Fig. 7. Female from the Hackness Rock of Scarborough, Yorkshire, England: SM J47113. Immature (?)phragmocone. *a*, side view; *b*, ventral view. Both ×1.

Fig. 8. Female from the Hackness Rock, Scarborough Castle Rock, Yorkshire, England: SM J5621. Mature(?) phragmocone. *a*, side view; *b*, ventral view. Both ×1.

All figures ×3 unless otherwise stated. Specimens have been whitened with ammonium chloride, except fig. 6 which has been whitened with magnesium oxide. All photographs by the author, all unretouched.



PALFRAMAN, *Distichoceras* from the Oxford Clay

their early developmental stages to those of *D. bicostatum* ♀ at a similar growth stage. They are small, rounded, alternate either side of the venter and the same density per whorl. After about half a volution of development, or one-eighth of a whorl before the beginning of the body chamber in adult specimens, the spines attain a relatively much larger size (see Pl. 10, figs. 1*a*, *d*, 2*a*, 3*a*, and 4*a*). At this stage the ventro-lateral spines become more angular and distant and instead of remaining on the ventro-lateral area, the median aspect of the spine bases extends on to the venter proper.

Ventral ridge. In consequence of the encroachment of the ventro-lateral spines on to the venter, the ventral ridge, which up to this stage remains clearly visible, completely disappears (see Pl. 10, figs. 1*b*, 2*c*, and 4*c*). From its development to its degeneration the ventral ridge is commonly straight unlike that of *D. bicostatum* ♀ which, though often straight at small diameters, has a tendency to be wrinkled on the final whorl of the phragmocone.

Lateral ornament. At no stage on a single observed specimen were there ribs to be seen: lateral ornament, however, is a common feature generally taking the form of either a fillet or groove or even a combination of these. Lateral grooves situated on the mid-flanks are undoubtedly more common than fillets. Grooves vary from narrow and distinct (see Pl. 9, fig. 6) through to shallow and less obvious (see Pl. 9, fig. 3*a* and Pl. 10, figs. 1*a* and *b*). In the case of specimen BM C15710, the broad lateral groove is flanked by levee-like elevations. Only one specimen (OUM J25687 was observed to have a combination of spiral grooves and fillets. They are very feeble and do not show up photographically even using a low-angled light source (see Pl. 9, fig. 5*a* and text-fig. 6A). Some specimens are perfectly smooth (see Pl. 10, fig. 2*a* and Pl. 11, fig. 1) or with very feeble spiral fillets (see Pl. 10, fig. 4*c*). On the flanks of the final phragmocone whorl of a well-preserved specimen (OUM J23247) is a series of very fine striae, similar in nature to those already described for specimen OUM J25684 (*D. bicostatum* ♀, cf. Pl. 11, fig. 3*d*).

Small, shallow, convex, crescentic pits are to be seen on the flanks of some specimens (see Pl. 9, fig. 4 and Pl. 10, fig. 3*a*). The pits begin either immediately before or shortly after the commencement of ventro-lateral spines and extend on to the body chamber.

Remarks. It is considered that the spiral fillets and grooves may be related more to the internal moulds of the specimens studied, by way of soft-part attachment areas, than true reflections of shell ornament. The same may well be true of the crescentic pits situated on the flanks.

Sutures

Sutural ontogeny. The prosuture of *D. bicostatum* ♂ is very different from all succeeding sutures, but almost identical to the prosuture of *D. bicostatum* ♀ (see text-fig. 8A and B). Extremely close similarity is also true of the primary suture of the supposed sexual dimorphs (see text-fig. 8C and D). Successive sutures develop new elements which are added in the umbilical region, U-type ontogeny, and become progressively more frilled and complex towards the adoral end of the phragmocone (see text-fig. 8).

Sutural variation. Sutural variation at a prescribed diameter, here arbitrarily chosen at about 9 mm., from randomly chosen specimens on which the sutures at this diameter are not degenerate, is seen to be small (text-fig. 10). The elements of the suture considered are the ventral and lateral lobe and the first and second lateral saddles. These are the most complex sutural elements at any diameter.

Remarks. The variation recorded may be due to any of the factors previously mentioned as influencing the sutural variation of *D. bicostatum* ♀. In addition, the relatively large spines of *D. bicostatum* ♂ and the degeneration of the ventral ridge at about this diameter may have an even greater sutural influence at both and intra- and inter-individual level, than in *D. bicostatum* ♀. Spath (1938), in his study of liparoceratid ammonites, recorded marked discordances between the form of adjacent sutures and also within the same suture on either side of the venter. Wide sutural variation was also demonstrated by Arkell (1957*b*) between otherwise identical specimens of the two species *Morrisiceras morrisi* (Oppel) and *Clydoniceras discus* (Sowerby). No such marked differences are recorded here for either *D. bicostatum* ♂ or ♀ in which even the most marked variation is very small and of the same order as that displayed by *Creniceras renggeri* (Oppel) ♂ and ♀ (Palframan 1966).

The mature phragmocone. Sutural approximation and degeneration, already considered here as a feature of maturity, can clearly be seen in many specimens (see Pl. 10, figs. 2*a* and 3*a* and Pl. 11, fig. 2). The diameter of its occurrence is from 7–17 mm. (see Table 1), with a mean of 12·2 mm.

Remarks. The six specimens (BM 37755, BM C10646, OUM J23246–7, BM C10644–5) now recorded in Table 1 (column M.S.D.(A)) were not discovered by the author until after the completion of text-figs. 3, 4, and 5 on which the mean diameter at which septation ceased in adult specimens ($\bar{d}_s$) is denoted as being 10·9 mm. However, as no measure-

EXPLANATION OF PLATE 12

Distichoceras bicostatum (Stahl)

Fig. 1. Male from the Oxford Clay, Summertown, Oxford, England: BM C10646. Side view, the final half whorl is body chamber. Note the ornamented spines of the body chamber. ×3.

Fig. 2. Male from the Lamberti Beds, Trockau, Bavaria: BM C40982. Side view, showing lappet. ×3.

Fig. 3. Female from the Hackness Rock, Scarborough Castle Rock, Yorkshire, England: SM J5619. Mature specimen with one-third of a whorl of body chamber. Side view, note the ribbing on to the lower flank of the body chamber.

Fig. 4. Male from the 'Brown Jura 3, Beuren, Württemberg', Germany: BMC 73644. Side view of almost complete adult with two-thirds of a whorl of body chamber. The adapertural body chamber termination is constricted and bears the beginnings of a lappet. ×3.

Fig. 5. Female from the Lamberti Limestone, Woodham, Bucks., England: OUM J20852. Badly crushed mature phragmocone. Side view.

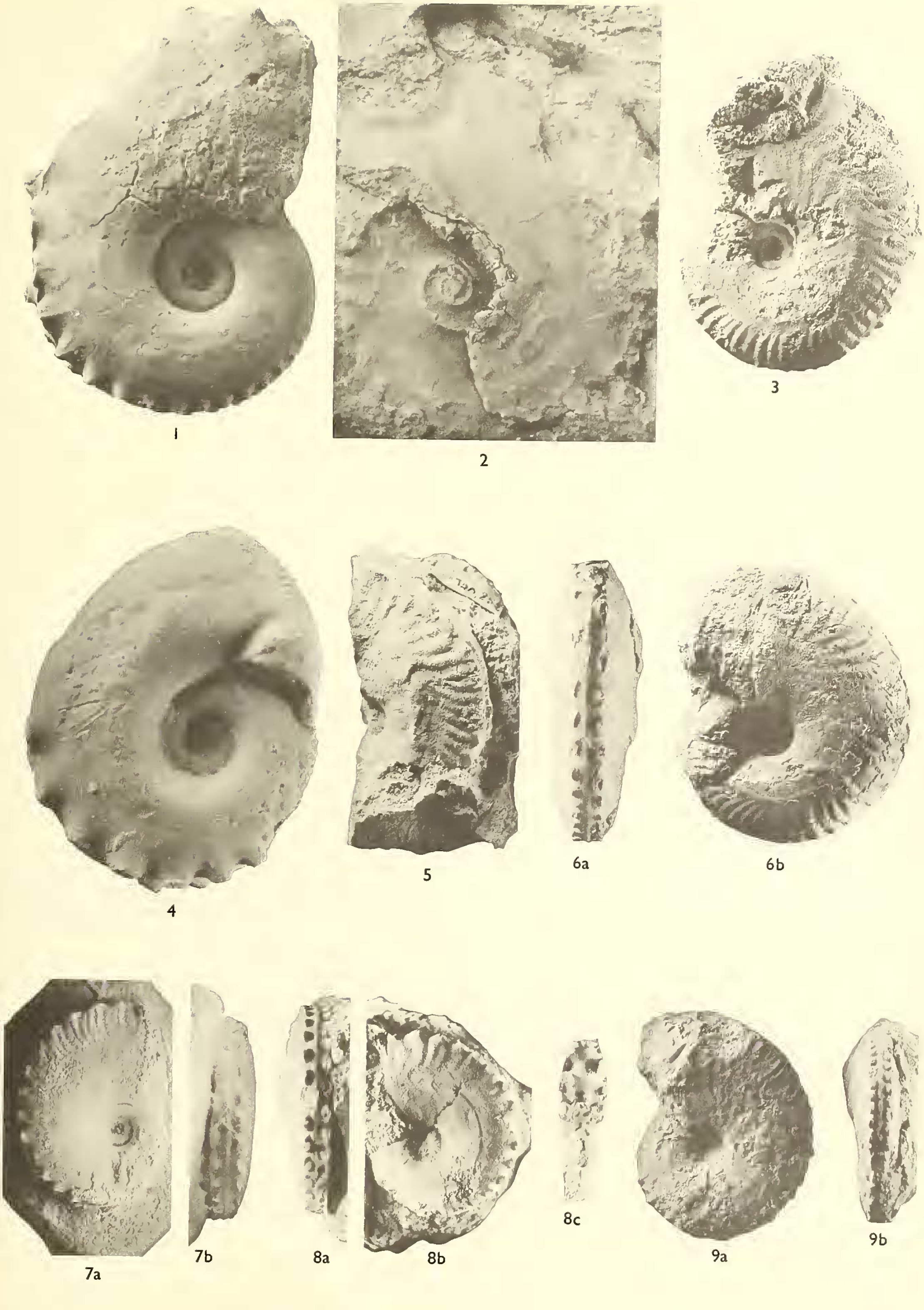
Fig. 6. Female from the Hackness Rock, Scarborough, Yorkshire, England: BM 39525. Mature specimen with about one-sixteenth of a whorl of body chamber. *a*, ventral view, note the weakening of the ventral ridge and the ventro-lateral spines towards the body chamber; *b*, side view, note the lateral fillet fading adorally.

Fig. 7. Juvenile(?) female from the Hackness Rock, Scarborough Castle Rock, Yorkshire, England: SM J5620. Phragmocone only. *a*, side view, note the presence of some non-looped ribs; *b*, ventral view.

Fig. 8. Female from the Hackness Rock, Scarborough, Yorkshire, England: BM 89044. Mature phragmocone. *a*, ventral view, showing well-developed ventral ridge; *b*, side view, showing well-developed looped ribs and lateral groove; *c*, cross-section of immature phragmocone.

Fig. 9. Female from the Hackness Rock of Gristhorpe, Yorkshire, England: SM J5623. Mature(?) specimen with one-eighth of a whorl of body chamber. *a*, side view; *b*, ventral view.

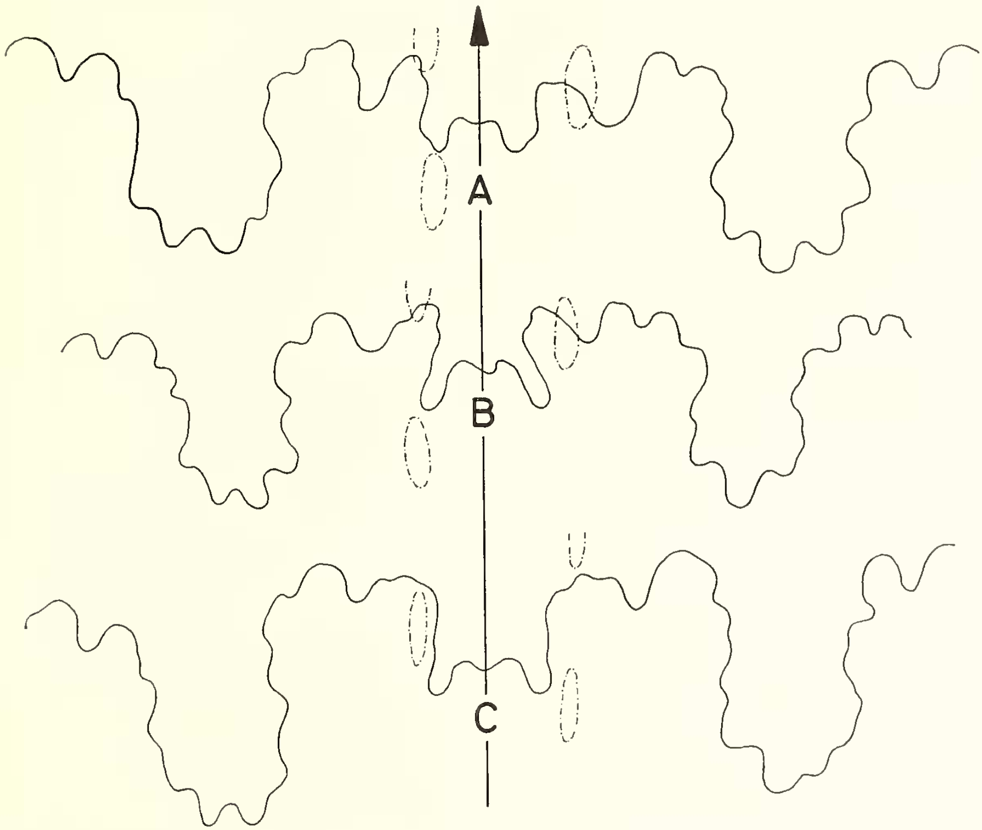
All figures ×1 unless otherwise stated. Specimens have been whitened with ammonium chloride, except figs. 1, 2, 4 which have been whitened with magnesium oxide. Photographs by the author, all unretouched.



PALFRAMAN, *Distichoceras* from the Oxford Clay

ments of these six specimens were plotted on any of the three graphs they are accurate as they stand.

No single phragmocone is sufficiently entire or well preserved to count the number of whorls. It is estimated, however, that from the proseptum to the end of the phragmocone in mature specimens there are betewen $5\frac{1}{4}$ and $5\frac{3}{4}$ complete whorls.



TEXT-FIG. 10. Sutural variation in *Distichoceras bicostatum* (Stahl). Males: A, OUM J25680 at D = 9·2 mm. from the Athleta/Lamberti Zone, Woodham, Bucks., England; B, BM C15710 at D = 8·5 mm. from the Athleta(?) Zone, Eye, near Peterborough, England; C, SM J34090 at D = 8·9 mm. from the Athleta/Lamberti Zone, Woodham, Bucks., England. The position of the spines is clearly marked (dot-dash lines). All figs. ×20.

BODY CHAMBER

Though no complete body chamber was examined among British specimens, several individuals had sufficient preserved to enable an over-all description to be undertaken. In most of these cases, however, preservation is not good. Specimens from Germany help considerably in the description of the peristome and in determining the length of the body chamber of adults.

General growth

General whorl shape of the body chamber differs little from that of the mature phragmocone. The angle made by the flanks on the former, however, is more acute (cf. text-fig.

7B and see Pl. 10, figs. 3*b* and 4*c*). The W/D and HH/D ratios decrease significantly in the late stages of growth (see text-figs. 3 and 5), the latter being accompanied by a complementary increase of the U/D ratio (see text-fig. 4). The whorl width is the first dimension to show negative allometry, at a mean diameter of about 10–11 mm. Uncoiling of the body chamber at the umbilical seam, a feature of maturity, begins at a mean diameter of about 14–16 mm., becoming very marked in adults after half a whorl of body chamber growth (see Pl. 10, figs. 2*a*, 3*a*, and 4*a*).

Ornament

Ventro-lateral spines. The enormous ventro-lateral spines are undoubtedly the most marked characteristic of the body chamber. They show positive allometry towards the end of the phragmocone and continue to increase relatively for about $\frac{1}{6}$–$\frac{1}{4}$ of a whorl on to the body chamber. The largest spines, measured radially, are in the order of 2–3 mm. They are generally rectiradial (Pl. 10, figs. 1*a*, 2*a*, 3*a*, and 4*a*), but may be feebly rursiradial (Pl. 11, fig. 6) and are much more distant than on the phragmocone. On the venter the alternating spine bases overlap the median line; a ventral view at this stage is reminiscent of a coarsely set saw (see Pl. 10, figs. 2*b* 2*c*, 3*c*, and 4*b*). The spines extend for about $\frac{1}{3}$–$\frac{1}{2}$ a whorl before dying out completely, having reached an acme $\frac{1}{6}$–$\frac{1}{4}$ of a whorl of body chamber growth in adults. The venter and ventro-lateral areas are smooth in the final stages of growth, the former being gently rounded (see Pl. 10, figs. 4*b* and 4*c*).

Remarks. D'Orbigny (1842–51) first figured and described the species *Ammonites Baugieri* (= *Horioceras baugieri* = *D. bicostatum* ♂), which, though incomplete, has a maximum diameter of 36 mm. (d'Orbigny ibid., pl. 158, fig. 5). The last figured whorl shows the spines at first becoming relatively larger, reaching an acme, and finally fading completely to give rise to a smooth venter and ventro-lateral areas. On the same plate (ibid., fig. 6) is figured an apertural view of the same (?) specimen, which shows the ammonite to be completely septate. Other illustrations of apertural views of ammonite specimens are figured by d'Orbigny (1842–51), which in side view are uncoiling at the umbilical seam and/or presenting highly modified ornament in the late stages of the outer whorl and

EXPLANATION OF PLATE 13

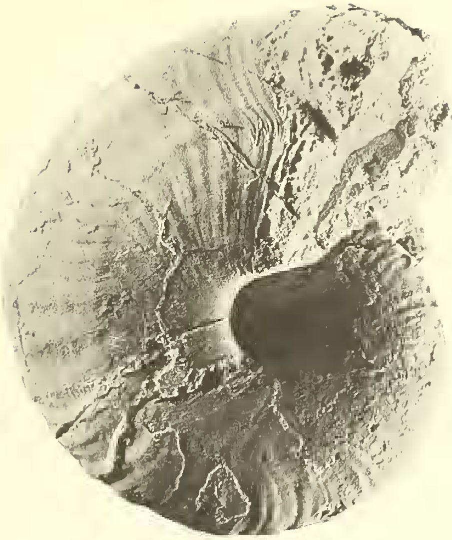
Distichoceras bicostatum (Stahl)

Fig. 1. Female from the Hackness Rock, Scarborough, Yorkshire, England: BM 50622. Complete adult. *a*, side view, note degenerate and approximated sutures, ribbing on the lower flank of the body chamber, and uncoiling of the body chamber at the umbilical seam; *b*, ventral view of the body chamber, note the absence of the ventral ridge and ventro-lateral spines and the continuous ribbing over the venter; *c*, apertural view, note the presence of both ventral ridge and ventro-lateral spines; *d*, side view showing the outline of the peristome; *e*, side view (reverse side of *a*) showing feather structure in original shell (×3).

Fig. 2. Female from the 'Scarborough Grey Limestone'(?) (probably the Hackness Rock), Scarborough, Yorkshire, England: BM C69282. Adult specimen with one-sixth of a whorl of body chamber. Side view showing well-developed fillet on the phragmocone which fades on the body chamber.

Fig. 3. Female from the Lamberti Limestone of Woodham, Bucks., England: OUM J20851. Side view of slightly crushed adult specimen with half a whorl of body chamber. Spines and looped ribs fade on the body chamber.

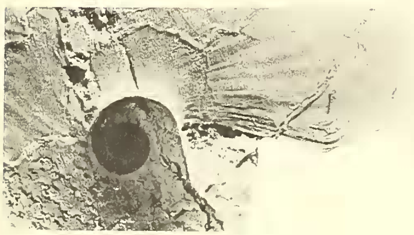
All figures ×1 unless otherwise stated. Specimens have been whitened with ammonium chloride. All photographs by the author, all un-retouched except fig. 1*d*.



1a

1b

1c



1d

1e

2

3

PALFRAMAN, *Distichoceras* from the Oxford Clay

which are drawn as still being septate. The author considers that these septa are imaginary rather than real and that d'Orbigny's figures (op. cit.—also reproduced by Arkell, Kummel, and Wright 1957, p. L280, figs. 327, 3*a* and 3*b*) are of a large mature specimen with perhaps the final half whorl being body chamber. The same figures also show the ventro-lateral spines of the last half whorl are notched by radial grooves which begin near the spine base: similar grooves have been seen on only one English specimen (BM C10646) from Summertown, Oxford (Pl. 12, fig. 1).

Lateral ornament. Lateral ornament is generally present, as indicated by d'Orbigny (1842–51), in various forms. A feeble fillet present on the phragmocone of specimen SM J34090, persists on to the body chamber (see Pl. 10, fig. 4*a*) as does the lateral groove of specimen BM C28327 (see Pl. 11, fig. 2). The poor preservation of body chambers, however, probably masks some of these delicate features. The small crescentic pits described as occurring on the phragmocone of specimen LU 265 continue on to the body chamber for about one-sixth of a whorl before completely fading (see Pl. 10, fig. 3*a*).

Remarks. As was suggested previously these pits may represent internal moulds of shell processes to which muscular attachment of the adapical soft parts of the creature was made.

Adult peristome

Quenstedt (1852, 1858, and 1886–7) figured several specimens of *Ammonites bidentatus* (= *D. bicostatum* ♂); in the two later works (ibid.) are figured adult specimens with apertural modifications (1858, pl. 70, fig. 10; 1886–7, pl. 85, figs. 17 and 18). One of these figured specimens (1886–7, pl. 85, fig. 17) has an unusually wide umbilicus which differs significantly from specimens examined here (see text-fig. 4). The second figure on the same plate (op. cit., fig. 18) has an umbilicus similar in size to those the author has examined from England: the unusually wide umbilicus mentioned may be due to preservation (the specimen appears to have been crushed) or to inaccurate drawing. The diameter of the phragmocone of these specimens is 11–12 mm., which falls within the range of material here examined, and have a maximum diameter of 18·5 to 22 mm. The final one-third of a whorl of body chamber is spineless and terminated by an ornate peristome. Immediately preceding the peristome is a feeble constriction which appears to be most marked ventrally. The actual peristome is slightly flared, the flaring weakening as it passes adorally on to a large spoon-shaped lappet (Quenstedt 1886–7, pl. 85, figs. 17 and 18 and herein text-fig. 11, inset). The point of contact between the lappet and body chamber is narrow, the lappet becoming wider, relative to the median plane, and rounded adorally. An apertural view (see text-fig. 11, inset 18*p*) shows that the lappets, which are concave relative to the median plane, converge adorally but do not quite meet. These complete specimens have a body chamber of between $\frac{5}{8}$–$\frac{2}{3}$ of a whorl in length. Two almost complete German specimens, BM C40982 from Trockau, Bavaria, and BM 73644 from Beuren, Württemberg, show that the body chamber comprises about two-thirds of a whorl. The interpretation of the crushed Bavarian specimen is somewhat tenuous, especially as the phragmocone is represented as an external mould only. However, there appears to be evidence of sutures, on this external mould, two-thirds of a whorl behind the peristome. Both these specimens have a constricted peristome (Pl. 12, figs. 2, 4); one of them (BM C40982, Pl. 12, fig. 2) bears a lappet which is in agreement, in both shape and size, with those illustrated by Quenstedt (1886–7 table 85, figs. 17, 18; reproduced herein text-fig. 11, inset). The most complete English specimens examined by the author, SM J34090 and BM 37755, have a little more than half a whorl of body chamber (Pl. 10, fig. 4*a* and Pl. 11, fig. 6) and show the spines completely fading adorally as on Quenstedt's complete figured specimens (op. cit.) and a German specimen illustrated herein (Pl. 12, fig. 4).

A fairly accurate estimate of the total number of whorls in complete mature specimens, counting from the proseptum, is between $5\frac{3}{4}$–$6\frac{1}{2}$.

Shell and muscle scars

No shell has been seen on specimens of *D. bicostatum* ♂ examined in the preparation of this paper: it is therefore impossible to describe any relationship between it and the internal moulds studied.

Remarks. Despite the lack of shell certain characteristics, which may be associated with the attachment of soft parts to the shell, have been noted. The muscle attachments recorded by Crick (1898) on two specimens of '*Distichoceras Baugieri*' (= *D. bicostatum* ♂) is parallel and near to the umbilical seam of the body chamber, swinging across the flank on to the venter near the junction between the body chamber and the phragmocone: no such attachment has been seen on material investigated here. The lateral ornament of the flanks, already described, may be associated with muscle attachment. In one juvenile specimen (OUM J14560), which has a quarter of a whorl of body chamber preserved, a sinuous elevation is present on the flank of the body chamber about one-eighth of a whorl from the last septum. This is strongest adorally on the mid-flank, weakening adapically towards the venter and umbilical seam (see Pl. 9, fig. 2*a* and text-fig. 6B), and may have been a temporary area of muscle attachment, which, had the creature grown, may have subsequently been infilled with secreted shell material. The 'attachment' is strongest in precisely the same position, mid-flank, as a series of pits already mentioned on specimen LU 265 (see Pl. 10, fig. 3*a*). It is also noteworthy that these pits do not continue beyond one-eighth of a whorl of the body chamber of the mature specimen where the soft parts of the creature may have been adapically attached.

DISCUSSION ON SEXUAL DIMORPHISM

Historical outline

Dimorphism in ammonoids has been recorded from the Devonian, the Jurassic, and the Cretaceous, though not all authors have necessarily considered this dimorphism to be sexual, Arkell (1957*a*) and Birkelund (1965) to mention but two. De Blainville (1840) appears to be the first author to mention sexual dimorphism in ammonites but gave no specific examples. The earlier workers, on the whole, preferred to compare only the adult stages of supposed sexual dimorphs, in which the small form with an ornate peristome was considered as being the male, the female being large and with a simple peristome (Munier-Chalmas 1892).

Shortly after the turn of the century the theory of sexual dimorphism in ammonites sank into relative obscurity only to be rejuvenated within the last ten years, due largely to the efforts of Callomon (1955, 1957, and 1963) and Makowski (1962).